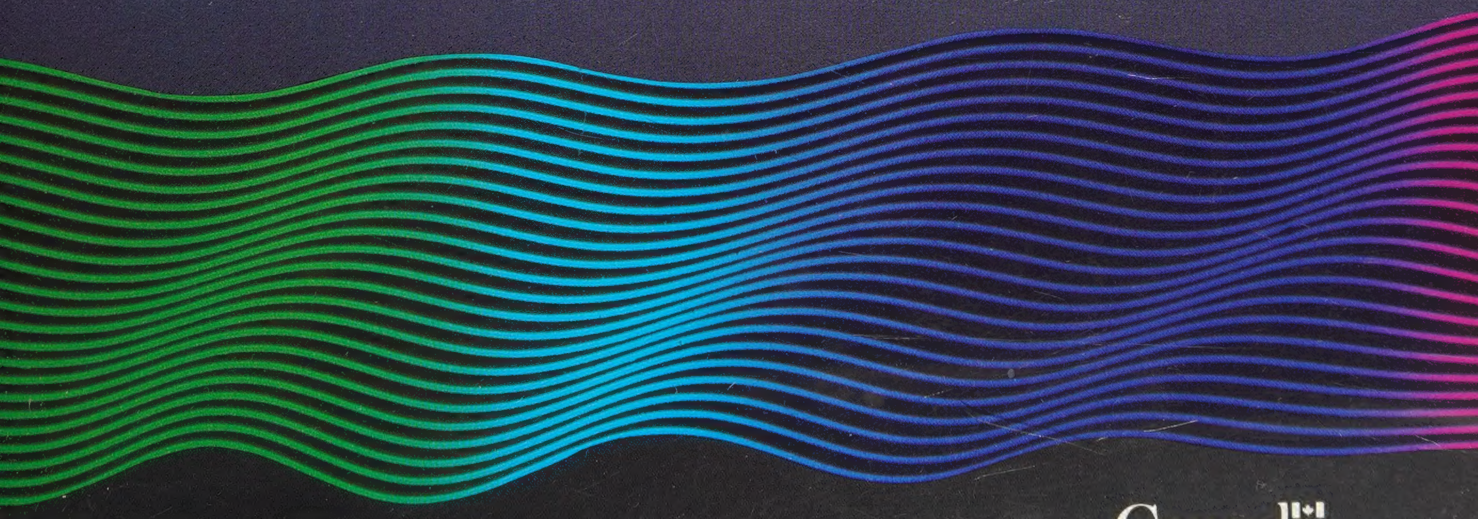
49(3)

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

APR 01 [illegible]
[illegible]



Fisheries and Oceans
Pêches et Océans

Canada

Scientific Excellence • Resource Protection & Conservation • Benefits for Canadians

Excellence scientifique • Protection et conservation des ressources • Bénéfices aux Canadiens

The *Canadian Journal of Fisheries and Aquatic Sciences* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37, and *Journal of the Fisheries Research Board of Canada* 1938–79.

Editorial Policy

The *Journal* publishes original research articles, critical reviews, perspectives (essays of opinion or hypothesis), and comments. Papers may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and they should lead to identifiable conclusions or syntheses, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of fisheries and aquatic sciences. They should demonstrate clearly a contribution to knowledge beyond the confirmation state. Originality should relate to more than the particular (a certain year, place, taxon, or chemical compound) such that existing understanding is reformulated or extended.

It would assist the Editors if prospective authors identified briefly by covering letter (a) aspects of their papers that meet the foregoing objectives, (b) potential referees, and (c) other manuscripts contemplated or in press containing the same or similar information.

Submissions in English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor. The *Journal* accepts no responsibility for statements made by contributors. The use of proprietary names does not imply endorsement of the product or company.

A page charge ($44 plus 7% GST) is made for manuscripts published. When submitting a manuscript, an author must state that the charge will be accepted.

Guides

A guide for authors and typists appears in the first issue of each volume and is available free from the *Journal*.

Subscriptions

The *Journal* is issued monthly to form annual volumes of twelve numbers plus Supplements. Orders and inquiries regarding subscriptions must be sent directly to Canada Communication Group — Publishing, Supply and Services Canada, Ottawa, Ontario, Canada K1A 0S9. Prepayment is required to the order of "The Receiver General for Canada."

Microfilm

Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, USA.

Typeset and
Printed in Canada by: The Runge Press Limited, Ottawa

Composé et
Imprimé au Canada par: The Runge Press Limited, Ottawa

Design: Ludvic Saleh & Associates, Ottawa

Conception graphique: Ludvic Saleh & Associates, Ottawa

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937 et *Journal de l'office des recherches sur les pêcheries du Canada* 1938–1979.

Politique de rédaction

Le *Journal* publie des articles fondés sur une recherche originale, des critiques, des essais portant sur une opinion ou une hypothèse (perspectives) et des commentaires. Les textes peuvent avoir trait aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influent sur les systèmes de production aquatique. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. Ils doivent clairement démontrer qu'ils contribuent aux connaissances en faisant plus que corroborer des faits. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles.

Les auteurs éventuels aideraient les rédacteurs s'ils identifiaient brièvement, dans une lettre d'accompagnement a) les aspects de leurs textes qui répondent particulièrement aux objectifs indiqués ci-dessus, b) des arbitres possibles et c) d'autres manuscrits envisagés ou sous presse, dont la teneur est identique ou se rapproche de celui qui est soumis.

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le *Journal* décline toute responsabilité quant aux énoncés des contributeurs. L'utilisation des noms de marques de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

Les manuscrits acceptés sont sujets à des frais de publication (44 $ plus 7% TPS). Quand un auteur présente un texte, il doit préciser que ces frais seront acceptés.

Guides

Le guide des auteurs et des secrétaires d'auteurs paraît dans la première livraison de chaque volume et est offert gratuitement par le *Journal*.

Abonnement

Le *Journal* paraît tous les mois, formant ainsi un volume de douze numéros, et offre en plus jusqu'à deux suppléments par année. On doit faire parvenir les commandes et demandes de renseignements concernant les abonnements au Groupe Communication Canada — Édition, Approvisionnements et Services Canada, Ottawa (Ontario), Canada K1A 0S9. Les paiements doivent être faits à l'avance à l'ordre du Receveur général du Canada.

Microfilms

On peut acheter sur microfilms de 16 ou 35 mm tous les numéros publiés depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, É.-U.

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 49, No. 3, March 1992

Volume 49, n° 3, mars 1992

Scientific Publications/Publications scientifiques

D. G. Cook, Ph.D.	*Editor/Rédacteur*
J. Camp/G. J. Neville/P. M. Burke/M. Milne	*Editorial and Publishing Services/Services de rédaction et d'édition*
P. E. K. Symons, Ph.D.	*Consulting Editor/Rédacteur-conseil (Victoria, B.C.)*

Associate Editors/Rédacteurs associés

C. D. Levings, Ph.D.	*Department of Fisheries and Oceans, West Vancouver*
J. D. Neilson, Ph.D.	*Department of Fisheries and Oceans, St. Andrews*
P. Schwinghamer, Ph.D.	*Department of Fisheries and Oceans, St. John's*
N. H. F. Watson, Ph.D.	*Department of Fisheries and Oceans, Halifax*
D. J. Noakes, Ph.D.	*Department of Fisheries and Oceans, Nanaimo*

LIBRARY

APR 01 1992

National Marine Fisheries Service
2570 Dole Street
Honolulu, Hawaii

Editorial Board/Conseil de rédaction

J. C. Roff	*University of Guelph*	(1990–1992)
L. M. Dickie	*Department of Fisheries and Oceans, Dartmouth*	(1990–1992)
R. M. Peterman	*Simon Fraser University*	(1992–1995)

Editorial Office:

Department of Fisheries and Oceans
Communications Directorate
Scientific Publications
200 Kent Street, 14th Floor
Ottawa, Canada K1A 0E6
Telephone (613) 993–2209
FAX (613) 990-1866

Bureau de rédaction :

Ministère des Pêches et des Océans
Direction générale des communications
Publications scientifiques
200, rue Kent, 14^{e} étage
Ottawa, Canada K1A 0E6
Numéro de téléphone (613) 993–2209
FAX (613) 990-1866

The *Journal* is abstracted or indexed in:/Le *Journal* est résumé ou signalé dans :

Aquatic Sciences and Fisheries Abstracts, Biological Abstracts, Chemical Abstracts, Current Awareness in Biological Sciences, Current Contents, FAO Freshwater and Aquaculture Contents Tables, FAO Marine Science Contents Tables, Oceanic Abstracts, and Science Citation Index

Statistical Analysis of Embedded Replicates in Mark–Recovery Experiments

Jon T. Schnute

Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada

Schnute, J. T. 1992. Statistical analysis of embedded replicates in mark–recovery experiments. Can. J. Fish. Aquat. Sci. 49: 432–442.

This paper examines statistical theory related to a specialized mark–recovery experiment in which a group of fish is marked with coded wire tags (CWTs) cut sequentially from a wire roll. If the roll contains several codes embedded repetitively and if fish are selected randomly for marking, the resulting marked group automatically comprises several random subgroups called "embedded replicate" groups. When the fish are recovered, each subgroup can be identified by a distinct mark. Consequently, embedded replication appears to offer an easy technique for extending the information available from a conventional CWT experiment with only one code. The paper contends, however, that embedded replicate groups inherently provide no useful information beyond that obtained by treating them as a single group. In particular, the use of embedded replicates for variance estimation can be deceptive. Analytical results supporting these claims are presented for two cases of special interest. The paper also provides an overview of statistical methods that can be used, without recourse to embedded replication, to assess uncertainty in parameters commonly measured by mark–recovery experiments.

L'auteur a appliqué une théorie statistique à une expérience spécialisée de récupération d'étiquettes dans laquelle un groupe de poissons ont été marqués par des étiquettes métalliques codées coupées en séquence d'un rouleau de fil métallique. Si le rouleau contient plusieurs codes répétitifs et si les poissons sont choisis au hasard pour l'étiquetage, le groupe de poissons ainsi étiquetés comprendra automatiquement plusieurs sous-groupes créés au hasard appelés « groupes de codes répétitifs ». Lorsque les poissons étiquetés sont récupérés, chaque sous-groupe peut être identifié par une étiquette particulière. Par conséquent, les codes répétitifs semblent constituer une méthode simple pour obtenir plus d'information lors d'une expérience classique d'étiquetage avec un seul code. L'auteur soutient cependant que les groupes de codes répétitifs ne fournissent pas en soi plus d'information utile que ne le fournit un groupe unique. Plus précisément, l'utilisation de codes répétitifs pour l'estimation de la variance peut être trompeuse. À cet effet, l'auteur présente des résultats analytiques de deux cas particulièrement intéressants étayant ces conclusions. Il présente aussi un aperçu des méthodes statistiques qui peuvent être utilisées, sans avoir recours à la méthode des codes répétitifs, pour évaluer l'incertitude liée aux paramètres communément quantifiés dans le cadre d'expériences de récupération d'étiquettes.

Received February 26, 1990
Accepted October 4, 1991
(JA489)

Reçu le 26 février 1990
Accepté le 4 octobre 1991

Since the early 1970s, coded wire tags (CWTs) have been used extensively to mark juvenile Pacific salmon for later recovery and identification. The resulting release and recovery information can be applied to hatchery operation, fishery management, and scientific research. For example, with the aid of CWTs, hatchery managers can assess juvenile survival to adulthood, and fishery managers can assess the impact of hatchery fish on a given fishery.

Kuhn et al. (1988) and Lapi et al. (1990) provide an overview of salmon CWT data collected on the North American Pacific coast. Each tag consists of a stainless steel segment, bearing an etched binary code. Tags are cut sequentially from a spool of wire by a machine that inserts them into the nose cartilage of juvenile salmon. For later recognition, the adipose fin is removed from each marked fish. Thus, in the recovery phase, fish with missing adipose fins can be examined for the presence of CWTs.

Typically, CWT data provide straightforward estimates of various quantities of interest. For example, suppose that 10% of a group of hatchery juveniles are marked and that, when these fish reach adulthood, seven of these marks appear in a 25% sample of a particular fishery. Then an estimated number of fish from the original hatchery group in the specified fishery is

$$(0.1) \qquad \frac{7}{0.10 \times 0.25} = 280.$$

Thus, the 1-in-10 marking rate and 1-in-4 sampling rate combine to give a total expansion factor of 40 for each marked fish.

Although estimates from CWT data are relatively straightforward, measures of variance can be more complex. Sampling may be stratified at various levels, and measurement errors may creep in from various sources, such as lost or misread tags. The problem, it would seem, is that only one estimate is available, while several are needed to measure variance.

Recently, salmon fishery agencies on the North American Pacific coast have begun to use special rolls of CWT wire, with several codes embedded repetitively on a single roll. When marking from such a roll is complete, the marked fish comprise equal groups, each bearing a distinct tag. By selecting fish randomly for marking, one obtains groups that represent random samples of the whole. These are called "embedded replicate" groups. They can be obtained easily, without changing the mechanics of marking. Incremental costs are relatively minor, associated with producing wire rolls of embedded codes and spending extra time in the decoding process.

Embedded replicates appear to provide a cheap, easy, empirical method of resolving the variance problem discussed above. Any statistic computed from CWT data is automatically measured multiple times, once for each embedded replicate group. Perry et al. (1990) document the rationale for this procedure and illustrate its use with data on marked fish from four Pacific hatcheries. Their arguments are compelling, and they correctly cite early recommendations of the Pacific Salmon Commission International Working Group on Mark–Recovery Statistics (of which I am a member) as support for their approach.

For illustration, consider a variant of the example leading to (0.1) in which marked fish are divided into two embedded replicate groups, so that each represents 5% of the juvenile population (for a total marking rate of 10% as before). Suppose that four marked fish from the fish group and three from the second appear as adults in a 25% sample of the fishery (for a total of seven tags as before). In this situation, a total expansion factor of

$$\frac{1}{0.05 \times 0.25} = 80$$

applies to each group, so that the two estimates $4 \times 80 = 320$ and $3 \times 80 = 240$ are obtained. These provide not only an overall mean estimate

$$(0.2) \quad \frac{240 + 320}{2} = 280,$$

as in (0.1), but also an estimated standard error

$$(0.3) \quad \sqrt{\frac{1}{2 - 1}\left[(320-280)^2 + (240-280)^2\right]} = 56.6.$$

The calculation (0.3) suggests that embedded replicates can be used to resolve an otherwise complex statistical problem. In any case, it is clear that nothing can be lost by using them, since they can always be treated analytically as though they were a single code. This paper argues, however, that variance estimates obtained from calculations like (0.3) can be deceptive. Furthermore, in the context of questions commonly addressed by CWT data, I show that embedded replicates provide no useful information beyond that obtained by treating them as a single code.

Section 1 of the paper presents intuitive arguments documenting my reasons for the above claims. Sections 2 and 3 give analytical results confirming these arguments in two special cases. Section 4 provides an overview of statistical methods for assessing uncertainty in estimates like (0.1), without recourse to embedded replicate data. The discussion includes reference to recent work by Clark and Bernard (1987), Geiger (1990), and Newman (1990). Section 5 applies these methods to six illustrative data sets and compares the results. Finally, section 6 summarizes the paper's conclusions.

1. Intuitive Arguments

Certain questions must be answered before building a statistical model for embedded replicates. What is a replicate? What are the implications of randomizing embedded codes among the marked population? What are the raw data, and what error structure exists among them? What is the purpose of the tagging experiment? Answers to such fundamental questions show that embedded replicates do not have the statistical properties which, at first, they seem to have. In this section, I present six intuitive arguments that illustrate some of the logical problems encountered in the analysis of embedded replicates.

First, multiple measurements, such as embedded replicates, are not generally needed to obtain variance estimates. For example, tagging experiments are often designed to measure a binomial probability p. Thus, if M marked fish are released from a hatchery and N are later recovered in a fishery, then

$$(1.1) \quad \hat{p} = \frac{N}{M}$$

estimates the recovery probability p in the given fishery for this marked group. It is well known for the binomial distribution (Mood and Graybill 1963, p. 263) that

$$(1.2) \quad \widehat{\sigma^2(\hat{p})} = \frac{\hat{p}\,(1 - \hat{p})}{M}$$

provides an estimate of $\sigma^2(\hat{p})$, the variance of $\hat{p}$. This example and the earlier one connected with (0.1) are discussed further in sections 2–5.

Second, whatever properties they may have, embedded replicates are definitely not true statistical replicates. In a properly designed experiment, some factors are deliberately controlled, while others are uncontrolled or even unknown. The purpose of replication is to identify variability associated with uncontrolled factors. Thus, replication consists of repeated, independent experiments subject to the same controls. By contrast, an experiment with embedded replicates involves no repetition. Rather, a single population is merely divided at random into a collection of subpopulations. Each subpopulation is exposed to the identical set of factors, both controlled and uncontrolled. Since embedded replicates do not constitute independent experiments, straightforward variance calculations like (0.3) may be inappropriate.

Third, even if the technique cannot be considered a form of true replication, it might be compared with the method of ''interpenetrating subsamples.'' Cochran (1977, p. 388) illustrated this method in the context of an opinion poll conducted by several interviewers. For example, if each of 10 interviewers is assigned 10% of the population at random, then variations among interviewers should theoretically be explainable by chance alone. Thus, interviewer bias could be detected by a lack of randommess among results reported by the 10 interviewers. Like interpenetrating subsamples, embedded replicates are also selected randomly; however, nonrandom results among embedded subgroups cannot be attributed to a known source analogous to an interviewer effect.

This argument leads naturally to the fourth point, which is that an embedded replicate experiment can lead to only two possible outcomes. Either embedded tag codes are distributed randomly among the recoveries or they are not. If they are, nothing new is learned; the experiment has only provided empirical verification of the laws of chance. If they are not, then still nothing is learned, since, by deliberate experimental design, no explanation is available for the departure from randomness. Thus, any extra costs associated with embedded replication would seem unjustified, regardless of the outcome of the experiment.

A fifth argument comes from contemplating a computer program to simulate the results of an embedded replicate experiment. Such a program would necessarily have two components: one to select embedded tag codes randomly and another to simulate the fate of marked and unmarked fish. Since marked fish are assigned embedded replicate codes at random, the second component of the program cannot reasonably alter the fate of a marked fish based on its embedded replicate code. Consequently, the same statistical simulation can be achieved by reversing the order of the program's two components: first simulate the fate of fish unmarked or marked with a single code and then allocate embedded codes randomly to the marked recoveries. In practice, this implies that statistical results of an embedded replicate experiment can equivalently be achieved by using only one tag code and applying computer simulation *after the experiment is complete* to distribute embedded codes randomly among marked recoveries. Thus, extra data from embedded replication must be useless, since the same information can equally well be simulated as obtained from the experiment itself. Sections 2 and 3 illustrate this result analytically in two contexts.

Finally, simple examples illustrate that embedded replicate codes cannot be used to detect all possible sources of variability in mark–recovery data. Consequently, calculations like (0.3) can be misleading. For example, suppose that 100 marked fish are caught in a fishery with five boats. If each boat catches 20 marked fish, this indicates low variability due to stratification at the level of individual boats. By contrast, if one boat catches all 100 marked fish, then variability would be high; it might have been a rare chance event that any marked fish were caught at all. Embedded replicates are incapable of detecting such variations in the recovery phase of the experiment, since they are applied randomly at the time of release. Thus, if the 100 marked fish include 10 embedded replicate codes, the distribution of these codes is independent of variability among recoveries by boat.

2. Binomial Likelihood

This section and the next present analytic examples that support the intuitive arguments cited above, particularly the fifth. In each section, I derive likelihood functions for experiments conducted with and without embedded replicate codes. Relationships between these likelihoods show that partitioning marked fish into embedded subgroups can equivalently take place either before release or after recovery.

In this section, I consider again the example (1.1)–(1.2) in which M marked fish are released from a hatchery and N are later recovered in a fishery. If marked fish are independently exposed to the recapture probability p, then the likelihood (probability) of N conditioned on M and p is simply the binomial distribution

$$(2.1)\quad L(N|M,p) = \binom{M}{N} p^N(1-p)^{M-N}$$

where

$$(2.2)\quad \binom{M}{N} = \frac{M!}{N!(M-n)!}.$$

The binomial experiment can be compared with a similar one that includes two embedded replicate codes. In this case, the M marked fish comprise two groups with M_i fish in each group ($i = 1, 2$) where

$$(2.3)\quad M = M_1 + M_2.$$

Let N_i ($i = 1, 2$) denote the number of fish from each group later recovered in the fishery, and define

$$(2.4)\quad N = N_1 + N_2.$$

Since fish in the embedded groups are assigned randomly, all are subject to the same recovery probability p, as before. Thus, the likelihood function for this experiment is the product of binomials

$$(2.5)\quad L(N_1, N_2|M_1, M_2,p) = \binom{M_1}{N_1} p^{N_1}(1-p)^{M_1-N_1}\binom{M_2}{N_2} p^{N_2}(1-p)^{M_2-N_2},$$

i.e. the probability of observing both N_1 and N_2 is the product of probabilities for each.

Taking account (2.3)–(2.4), a short calculation shows that (2.5) can be rewritten as

$$(2.6)\quad L(N_1, N_2|M_1, M_2, p) = L(N_1, N_2|M_1, M_2, N)\, L(N|M, p)$$

where $L(N|M, p)$ is the binomial likelihood (2.1) and

$$(2.7)\quad L(N_1, N_2|M_1, M_2, N) = \binom{M_1}{N_1}\binom{M_2}{N_2} \bigg/ \binom{M}{N}$$

is the hypergeometric likelihood associated with the distribution of N_1 and N_2 marked fish among the total of N marked recoveries. For the example here, (2.6) provides rigorous proof of the fifth intuitive argument in section 1. The statistics of an embedded replicate experiment are the same if either (A) replicate marks are randomly distributed among released fish or (B) assignments are made to replicate groups among recoveries after the experiment is complete. Likelihood functions for scenarios A and B are given by the left and right sides of (2.6), respectively.

Another consequence of (2.6) is that likelihood inferences about p in this context depend only on the totals M and N in (2.3)–(2.4), not on the separate numbers M_1, M_2, N_1, and N_2. This is true because the function $L(N_1, N_2|M_1, M_2, N)$ in (2.6) is independent of p. Thus, the likelihoods $L(N_1, N_2|M_1, M_2, p)$ and $L(N|M, p)$ are the same except for a factor independent of p. In statistical language, the totals M and N are sufficient for p.

A skeptic might argue that this analysis is flawed because it assumes that both replicate groups have the same recovery probability p. If, instead, the two groups have different probabilities p_i ($i = 1, 2$) of recovery, then (2.5) would be replaced by

$$(2.8)\quad L(N_1, N_2|M_1, M_2, p_1, p_2) = \binom{M_1}{N_1} p_1^{N_1}(1-p_1)^{M_1-N_1}\binom{M_2}{N_2} p_2^{N_2}(1-p_2)^{M_2-N_2}.$$

In (2.8), M and N alone are not sufficient for inferences on the parameter pair (p_1, p_2). Furthermore, a likelihood ratio test based on (2.8) could be used to test the null hypothesis

$$(2.9)\quad H_0 : p_1 = p_2$$

against the alternative

TABLE 1. Notation for models of sampled catch. The upper portion of the table relates to an experiment with only one mark. The lower portion assumes the use of two embedded replicate codes.

	Mark rate	Catch	Sample
One code			
Marked	p	N	X
Hatchery total		M	
All fish		C	S
Two codes			
Marked group 1	$p/2$	N_1	X_1
Marked group 2	$p/2$	N_2	X_2
Marked total	p	N	X
Hatchery total		M	
All fish		C	S

(2.10) $H_1 : p_1 \neq p_2$.

However, as discussed in section 1, there are only two possible outcomes to such a test: either the data support rejecting H_0 or they do not. If not, then the laws of chance are confirmed experimentally, the likelihood (2.1) applies, and nothing new is learned from embedded replication. If so, then again nothing new is learned because the experiment provides no explanation for the statistical difference between p_1 and p_2. By design, no experimental distinction exists between the embedded codes.

In spite of these arguments, a skeptic might contest that embedded codes could at least be used to devise a test of model adequacy. For example, the binomial model might be inappropriate if fish exhibit clustering behaviour that induces correlations among recoveries of individual fish. Perhaps a statistical difference between p_1 and p_2 would provide evidence for this. However, since embedded codes are applied randomly, their recoveries should still occur randomly in the two recovery groups, irrespective of clustering behaviour. Indeed, the likelihood function (2.8) is inappropriate for clustering behaviour, since it assumes independence between the two embedded groups. Thus, (2.8) serves to illustrate a statistical model that incorrectly mirrors experimental reality. As discussed in section 1, an appropriate model must give equivalent statistical treatment to fish with different embedded codes.

3. Sampled Catch Likelihood

The problem leading to the estimate (0.1) in the introduction is more complex analytically than the binomial example above. Table 1 summarizes the notation necessary for a full description, either with one tag code or with two embedded replicates.

To state the problem with one tag code exactly, suppose that a group of hatchery fish are marked at a known rate p. After these fish are released and grow to adulthood, suppose that X marked fish from the group are recovered in a sample of S fish taken from a fishery with a total catch of C fish. Given the data (X, p, C, S), consider the problem of trying to estimate M, the total number of hatchery fish in the catch. In addition to M, another unknown quantity in this situation is the number N of marked fish in the catch. To be consistent with the description here, the six numbers listed in the upper portion of Table 1 must be constrained by

(3.1) $0 \leq X \leq N \leq M \leq C$

(3.2) $X \leq S \leq C$

(3.3) $0 \leq p \leq 1$.

The likelihood function for this scenario necessarily involves two processes: (A) the distribution of N marked fish among M hatchery fish and (B) the selection of X marked fish when sampling a population that includes N marked fish. Assuming that the fishery is not selective between marked and unmarked fish, the original binomial marking proportion p becomes a binomial probability for marks in the catch. Thus, the likelihood function for process A is

$$(3.4) \quad L(N|M, p) = \binom{M}{N} p^N (1 - p)^{M-N},$$

as in (2.1). Process B involves sampling without replacement; consequently, it is governed by the hypergeometric distribution (Pollard 1977, p. 118–119)

$$(3.5) \quad L(X|N, C, S) = \binom{N}{X}\binom{C-N}{S-X} \Big/ \binom{C}{S}$$

associated with sampling both marked and unmarked fish.

In (3.4)–(3.5), the result N from process A acts as input to process B. Consequently, by (3.1), the probability distribution of X depends on all values N between X and M. To be precise, the likelihood is the following sum of products of (3.4)–(3.5):

$$(3.6) \quad L(X|M, p, C, S) = \sum_{N=X}^{M} \binom{M}{N} p^N (1-p)^{M-N} \binom{N}{X}\binom{C-N}{S-X} \Big/ \binom{C}{S}$$

where

(3.7) $0 \leq X \leq \min(S, M)$.

The range of X in (3.7) takes account of (3.1)–(3.2).

It can be shown from properties of the binomial and hypergeometric distributions that

$$(3.8) \quad \sum_{X=0}^{\min(S,\, M)} L(X|M, p, C, S) = 1.$$

Thus, the likelihood (3.6) defines a probability distribution, commonly called a "compound" distribution because it results from composing two random processes. Various authors (Clark and Bernard 1987; Geiger 1990; Newman 1990) have discussed the use of compound binomial–hypergeometric distributions in the analysis of CWT data. The same distribution can occur in different contexts. For example, Newman (1990) describes an experiment leading to (3.6) in which M is given and p is the unknown parameter.

As in section 2, the experiment with a single code can be compared with a similar experiment with two embedded codes. Table 1 summarizes the notation required for this extended analysis. Again, a sample of size S is taken from the total catch C. Two embedded marked groups occur within this sample, each originally marked at the rate $p/2$. Thus, the combined mark rate for both groups is p, as before. The quantity X_i denotes the number of observed recoveries from group i ($i = 1, 2$), so that

(3.9) $X = X_1 + X_2$

again represents the total number of marked fish in the sample. The problem now is to estimate the total number M of hatchery fish from the available data (X_1, X_2, p, C, S). Unknown intermediate quantities include various numbers of marked fish within the catch C: N_i from group i ($i = 1, 2$) and the total

(3.10) $N = N_1 + N_2$.

Given the definitions (3.9)–(3.10), data for this problem are constrained by (3.1)–(3.3) and

(3.11) $0 \leq X_i \leq N_i \qquad (i = 1, 2)$.

As before, the likelihood function for resolving this problem results from two processes. First, three groups of fish (two marked groups and one unmarked) are multinomially distributed with probabilities determined by proportions released from the hatchery; thus,

$$(3.12) \quad L(N_1, N_2|M, p) = \binom{M}{N_1\, N_2} (p/2)^{N_1}(p/2)^{N_2}(1-p)^{M-N_1-N_2}$$

where

$$(3.13) \quad \binom{M}{N_1\, N_2} = \frac{M!}{N_1!N_2!(M-N_1-N_2)!}$$

denotes a multinomial coefficient. Second, these three groups in the catch are distributed within the sample by the multivariate hypergeometric distribution

$$(3.14) \quad L(X_1, X_2|N_1, N_2, C, S) = \binom{N_1}{X_1}\binom{N_2}{X_2}\binom{C-N_1-N_2}{S-X_1-X_2} \bigg/ \binom{C}{S}.$$

Since the random pair (N_1, N_2) is output from the first process and input to the second, the final likelihood function is a sum of products of (3.12) and (3.14) over all possible values (N_1, N_2):

$$(3.15) \quad L(X_1, X_2|M, p, C, S) = \sum_{N_2=X_2}^{M-X_1} \sum_{N_1=X_1}^{M-N_2} \binom{M}{N_1\, N_2} (p/2)^{N_1}(p/2)^{N_2}(1-p)^{M-N_1-N_2} \times \binom{N_1}{X_1}\binom{N_2}{X_2}\binom{C-N_1-N_2}{S-X_1-X_2} \bigg/ \binom{C}{S}.$$

The summation ranges in (3.15) are determined by the constraints (3.1), (3.2), and (3.11).

Appendix A proves that the likelihood (3.15) can also be written as

$$(3.16) \quad L(X_1, X_2|M, p, C, S) = L(X_1|X)\, L(X|M, p, C, S)$$

where $L(X|M, p, C\ S)$ is the likelihood (3.6) associated with the total number of recoveries X and

$$(3.17) \quad L(X_1|X) = \binom{X}{X_1} 2^{-X}$$

is the distribution of recoveries X_1 from marked group 1 for a given total number of recoveries X. Since

$$2^{-X} = (1/2)^{X_1}(1/2)^{X_2},$$

(3.17) represents a binomial distribution in which both marked groups 1 and 2 occur with the same probability 1/2.

The result (3.16) for this example is analogous to (2.6) in section 2. Both equations confirm the fifth intuitive argument in section 1; that is, the distribution of marks between embedded replicate groups can equivalently be made either before or after the experiment is complete. Either method leads to the same likelihood function. In the present context, (3.16) shows that the total number of recoveries X is sufficient for the unknown parameter M, since M occurs only in the factor $L(X|M, p, C, S)$. Furthermore, following the logic of the fourth argument in section 1, the use of embedded replicates here can lead to only two possible outcomes. Either the split between X_1 and X_2 conforms to the distribution (3.17) or it does not. If so, then the experiment would merely confirm the binomial law (3.17). If not, then the experimenter could statistically reject a 50/50 split between X_1 and X_2. Since the embedded codes were originally applied with the same mark rate $p/2$, the experiment would offer no explanation for this peculiar outcome.

TABLE 2. Statistical inference methods for questions 1 and 2, showing the equations used to compute $\hat{\theta}$, $\widehat{\sigma(\hat{\theta})}$, and (θ_-, θ_+). Where required, the relevant likelihood function $L(\theta)$ is also indicated. Computations marked with an asterisk are performed using $\alpha = 95\%$.

Method	Label	Question	θ	$L(\theta)$	$\hat{\theta}$	$\widehat{\sigma(\hat{\theta})}$	(θ_-, θ_+)
Analytic variance	AV	1	p	—	(4.4)	(4.6)	(4.1)
Analytic variance	AV	2	M	—	(4.7)	(4.8)	(4.1)
Exact interval	EI	1	p	—	(4.4)	(4.3)*	(4.9)
Likelihood variance	LV	1	p	(2.1)	(4.12)	(4.13)	(4.1)
Likelihood variance	LV	2	M	(3.6)	(4.12)	(4.13)	(4.1)
Likelihood interval	LI	1	p	(2.1)	(4.12)	(4.3)*	(4.14)
Likelihood interval	LI	2	M	(3.6)	(4.12)	(4.3)*	(4.14)
Approximate AV	AAV	2	M	—	(4.7)	(4.18)	(4.1)
Approximate LI	ALI	2	M	(4.15)	(4.12)	(4.3)*	(4.14)

4. Statistical Inference

If embedded replicates are not appropriate for measuring uncertainty, then it remains to articulate methods that can be used instead. In this paper, I confine my discussion to the two questions raised in sections 2 and 3, namely:

QUESTION 1. If M marked fish are released from a hatchery and N are later recovered in a fishery, what is an estimate of the recovery probability p?

QUESTION 2. Suppose that X fish from a marked group are recovered in a sample of size S taken from a total catch C. If this group represents hatchery fish originally marked at rate p, what is an estimate of the total number M of hatchery fish in the catch?

Each question involves finding an estimate $\hat{\theta}$ of an unknown parameter θ where $\theta = p$ and $\theta = M$ in questions 1 and 2, respectively. A complete answer should also include a method of assessing the uncertainty in $\hat{\theta}$.

This section briefly reviews various methods that have been proposed for answering such questions. For convenience, I adopt the names and labels summarized in Table 2. The methods fall into two categories, according to the technique used for assessing uncertainty. "Variance" methods give an estimate $\widehat{\sigma(\hat{\theta})}$ of the standard error $\sigma(\hat{\theta})$ in the estimate $\hat{\theta}$. "Interval" methods provide an α-level confidence interval (θ_-, θ_+) for the parameter θ at any specified probability level α. The two approaches can be related to each other by defining confidence intervals from standard errors and vice versa.

For example, if a variance method gives the estimate $\widehat{\sigma(\hat{\theta})}$, then an approximate α-level confidence interval (θ_-, θ'_+) for θ is determined by

$$(4.1) \quad \theta_{\pm} = \hat{\theta} + \nu(\beta_{\pm})\widehat{\sigma(\hat{\theta})}$$

TABLE 3. First- and second-order moments of (B) the binomial distribution (2.1) or (3.4), (H) the hypergeometric distribution (3.5), and (B-H) the compound binomial–hypergeometric distribution (3.6).

Distribution	Moment (expected value or variance)
B	$E[N] = Mp$
B	$V[N] = Mp(1-p)$
H	$E[X] = \dfrac{SN}{C}$
H	$V[X] = \dfrac{SN(C-N)(C-S)}{C^2(C-1)}$
B-H	$E[X] = \dfrac{pSM}{C}$
B-H	$V[X] = \dfrac{pSM}{C(C-1)}\left[C-pS-p\left(1-\dfrac{S}{C}\right)M-(1-p)\right]$

where $\nu(\beta)$ denotes upper β-point for a standard normal distribution and

$$(4.2)\quad \beta_{\pm} = \frac{1 \pm \alpha}{2}.$$

The end points (4.1) are based on the asymptotic result that $\hat{\theta}$ is approximately normal with mean θ. In particular, the following results hold when $\alpha = 95\%$: $\beta_{-} = 2.5\%$, $\beta_{+} = 97.5\%$, and $\nu(\beta_{\pm}) = \pm 1.96$. Thus, (4.1) takes account of the familiar result that 95% of a standard normal distribution lies in the interval $(-1.96, 1.96)$.

The interval (4.1) is symmetric about the estimate $\hat{\theta}$. In general, interval methods do not lead to such symmetry. Nevertheless, it follows from (4.1) that

$$(4.3)\quad \widehat{\sigma(\hat{\theta})} = \frac{\theta_{+} - \theta_{-}}{\nu(\beta_{+}) - \nu(\beta_{-})};$$

thus, the interval width $\theta_{+}-\theta_{-}$ provides a measure of uncertainty in $\hat{\theta}$. I use (4.3) as a convenient means of relating interval methods to variance methods. Since the right side of (4.3) may depend on the choice of α, I use $\alpha = 95\%$ as the standard for computing $\widehat{\sigma(\hat{\theta})}$ by an interval method.

With these preliminaries complete, I begin a detailed discussion of each method listed in Table 2. The ''analytic variance'' (AV) method requires analytic expressions for the expected value and variance of the underlying distribution. Table 3 shows the results needed for the questions posed here. For example, N in question 1 conforms to the binomial distribution (2.1). Equating the observation N to its expected value Mp gives the usual binomial estimate

$$(4.4)\quad \hat{p} = \frac{N}{M}.$$

Furthermore, since $\hat{p}$ is proportional to N, the variance of $\hat{p}$ is proportional to the variance of N; specifically, $V[\hat{p}] = V[N]/M^2$. Thus,

$$(4.5)\quad \sigma^2(\hat{p}) = \frac{p(1-p)}{M}$$

where $\sigma(\hat{p})$ denotes the standard error of $\hat{p}$. Substituting $\hat{p}$ for p in the right side of (4.5) gives the classical estimate

$$(4.6)\quad \widehat{\sigma(\hat{p})} = \sqrt{\frac{\hat{p}(1-\hat{p})}{M}}$$

cited earlier in (1.2). The results (4.4) and (4.6) provide the AV answer to question 1.

Similar logic can be used to resolve question 2. In this case, X conforms to the compound binomial–hypergeometric distribution (3.6). Analytical expression for $E[X]$ and $V[X]$ are shown in Table 3 and derived in Appendix B. Equating the observation X to its expected value pSM/C gives the estimate

$$(4.7)\quad \hat{M} = \frac{C}{pS}X.$$

In the language of CWT users, this represents an ''expansion'' of X by the inverse mark rate $1/p$ and the catch–sample ratio C/S. Since $\hat{M}$ is proportional to X, the variance $V[\hat{M}]$ can be computed from $V[X]$. As in the binomial example, this leads to the estimate

$$(4.8)\quad \widehat{\sigma(\hat{M})} = \sqrt{\frac{C\hat{M}}{pS(C-1)}\left[C-pS-p\left(1-\frac{S}{C}\right)\hat{M}-(1-p)\right]}$$

where $\sigma(\hat{M})$ denotes the standard error of $\hat{M}$. Thus, the AV answer to question 2 is contained in (4.7) and (4.8).

As discussed above, the AV method gives approximate confidence intervals via (4.1)–(4.2). For questions like those posed here, in which one parameter (p or M) is estimated from one statistic (N or X), an exact theory of confidence intervals can be developed (Mood and Graybill 1963, p. 256–262). When applied to the binomial distribution, the theory gives analytical expressions for the end points of an exact α-level confidence interval (p_{-}, p_{+}) for the parameter p in question 1 (Pollard 1977, p. 214):

$$(4.9)\quad p_{\pm} = \frac{(N+1)F_{\pm}}{M-N+(N+1)F_{\pm}}$$

where

$$(4.10)\quad F_{\pm} = F(\beta_{\pm}, 2(N+1), 2(M-N)),$$

$\beta_{\pm}$ is given by (4.2), and $F(\beta, m, n)$ denotes the upper β-point for the F distribution with m and n degrees of freedom (df). Thus, (4.9)–(4.10) constitutes the ''exact interval'' (EI) answer to question 1, where the estimate (4.4) still applies. A similar method, with less elegant formulas, could be derived for question 2, but I do not investigate it here.

The ''likelihood variance'' (LV) and ''likelihood interval'' (LI) methods in Table 2 depend directly on the likelihood function $L(\theta)$, where (2.1) and (3.6) define the likelihoods for questions 1 and 2, respectively. For example, $L(p) = L(N|M, p)$ in question 1; thus, L is considered a function of p alone, and the remaining data M and N are considered constants. The likelihood methods can be expressed conveniently in terms of the negative log likelihood

$$(4.11)\quad \ell(\theta) = -\log(L(\theta)).$$

Both LV and LI use the estimate $\hat{\theta}$ obtained by maximizing $L(\theta)$ or, equivalently, minimizing $\ell(\theta)$. Thus, $\hat{\theta}$ is determined by

$$(4.12)\quad \ell(\hat{\theta}) = \min_{\theta} \ell(\theta).$$

The LV method estimates $\sigma(\hat{\theta})$ by the formula

TABLE 4. Illustrative data for questions 1 and 2. Examples 1a–1c pertain to question 1, while 2a–2b pertain to question 2. In each case, a question mark indicates the parameter to be estimated.

Example	M	N	p	C	S	X
1a	1000	7	?			
1b	1000	70	?			
1b	1000	993	?			
2a	?		0.1	400	100	7
2b	?		0.4	400	100	7
2c	?		0.1	4000	1000	70

$$(4.13)\quad \widehat{\sigma(\hat{\theta})} = \left[\left. \frac{\partial^2 \ell}{\partial \theta^2} \right|_{\theta=\hat{\theta}} \right]^{-1/2},$$

which follows theoretically from asymptotic properties of $\hat{\theta}$ in (4.12) (Kendall and Stuart 1979, p. 46–47). The LI method uses the equation

$$(4.14)\quad \ell(\theta_{\pm}) - \ell(\hat{\theta}) = \frac{1}{2}\,\chi^2(\alpha, 1)$$

where $\chi^2(\alpha, 1)$ denotes the upper α-point for the χ^2 distribution with 1 df. In general, (4.14) has two roots θ_- and θ_+ that define an approximate α-level confidence interval (θ_-, θ_+). Theoretical justification for (4.14) comes from a likelihood ratio test (Kendall and Stuart 1979, Chap. 24).

Table 2 includes two approximate methods specific to question 2. Intuitively, it seems reasonable that the process of recovering X marks from a sample of M hatchery fish could be approximated by a single binomial process with probability pS/C, i.e. the product of the mark rate p and the sampling fraction S/C. This logic suggests the following simple approximation to the likelihood (3.6):

$$(4.15)\quad L(X|M, p, C, S) \approx \binom{M}{X}\left(\frac{pS}{C}\right)^{X}\left(1-\frac{pS}{C}\right)^{M-X}.$$

Computationally, (4.15) is more efficient than (3.6), since the latter involves a potentially large summation. The LI method for question 2 can be implemented using (4.15) in place of (3.6), and I refer to this variant as the "approximate LI" (ALI) method. Furthermore, treating (4.15) as exact binomial distribution for X leads to the moment equations

$$(4.16)\quad E[X] = \frac{pSM}{C}$$

$$(4.17)\quad V[X] = \frac{pS}{C}\left(1-\frac{pS}{C}\right)M.$$

Applying the AV method to (4.16)–(4.17) gives the estimate $\hat{M}$ in (4.7), as well as the error estimate

$$(4.18)\quad \widehat{\sigma(\hat{M})} = \sqrt{\frac{\hat{M}}{pS}(C-pS)}.$$

Thus, (4.7) and (4.18) constitute a variant of the AV method for question 2, based on the approximation (4.15). I refer to this as the "approximate AV" (AAV) method. Comparing (4.18) with (4.8) shows precisely how the AAV method simplifies the AV error estimate.

5. Examples

To compare the inference methods described above, I use the illustrative data presented in Table 4. I include three examples for each question, where example 2a corresponds to the sample calculation (0.1). Table 5 summarizes the results obtained by applying the methods in Table 2 to the examples in Table 4. For simplicity, I treat M in question 2 as a continuous (rather than integer-valued) parameter. Also, I simplify the language in this section by using the phrase "inference interval" in place of "approximate confidence interval"; thus, different inference methods produce different intervals. Appendix C provides details of numerical methods used in the analyses.

For question 1, the AV and LV methods give identical results. Analytically, (4.12) reduces to (4.4) for the binomial parameter $\theta = p$; similarly, (4.13) reduces to (4.6). For this reason, the AV and LV results appear on one line for each example 1a–1c. Although this analytical result is not true for question 2, the AV and LV methods still produce very similar results. For example 2c, they agree to the number of decimal places reported in Table 5. In general, the LV estimate $\hat{M}$ in question 2 is slightly lower than the commonly used AV estimate (4.7), as discussed in a different context by Schnute (1983, p. 2158).

Figure 1 illustrates the LI method (4.12) and (4.14) applied to example 1a. The minimum value $\ell(p)$ occurs at the estimate $\hat{p} = 0.007$ where $\ell(\hat{p}) = 1.90$. Dotted lines in Fig. 1 illustrate how the condition

$$(5.1)\quad \ell(p_{\pm}) = \ell(\hat{p}) + \frac{1}{2}\chi^2(0.95, 1) = 3.82$$

determines the end points of the 95% inference interval

$$(5.2)\quad (p_-, p_+) = (0.0030, 0.0135)$$

reported in Table 5 for example 1a (LI). Figure 2 carries the analysis one step further by plotting α as a function of p from the following variant of (4.14):

$$(5.3)\quad \chi^2(\alpha, 1) = 2[\ell(\theta) - \ell(\hat{\theta})]$$

where $\theta = p$. Thus, the two points with $\alpha = 0.95$ on the curve in Fig. 2 also determine the interval (5.2). More generally, the left and right branches of this curve determine an α-level inference interval for any α between 0 and 1, where the interval widens as α approaches 1.

Figure 3 illustrates the LI method applied to example 2a, i.e. the introductory example (0.1). The figure shows the function $\ell(M)$ obtained from both the exact likelihood (3.6) and its approximation (4.15). Since the two curves are close, the LI and ALI methods give similar results for example 2a (Table 5). This proximity is also evident in Fig. 4, which is obtained from (5.3) with $\theta = M$.

Regardless of the inference method, example 2a shows that a 95% inference interval can be restricted by a biological constraint. In this case, by (3.1), the number M of hatchery fish cannot exceed the total catch $C = 400$. Thus, the curves in Fig. 3 and 4 are truncated at $M = 400$, and the LI and ALI intervals reported for example 2a in Table 5 both have upper limits $M_+ = 400$. Furthermore, the variance methods all produce an estimate $\widehat{\sigma(\hat{\theta})}$ so large that the 95% interval (4.1) has $M_+ > 400$. Thus, (4.1) is inappropriate for this case. Instead, the constraint (3.1) determines $M_+ = 400$, and M_- is computed from the following one-sided counterpart of (4.1):

TABLE 5. Parameter estimates $\hat{\theta}$, estimated standard errors $\widehat{\sigma(\hat{\theta})}$, and 95% inference intervals (θ_-, θ_+) for the examples in Table 4, based on the methods in Table 2. One-sided inference intervals are used in the calculations for example 2a.

Example	Method	θ	$\hat{\theta}$	$\widehat{\sigma(\hat{\theta})}$	95% interval
1a	AV, LV	p	0.0070	0.0026	(0.0018, 0.0122)
1a	EI	p	0.0070	0.0028	(0.0034, 0.0143)
1a	LI	p	0.0070	0.0027	(0.0030, 0.0135)
1b	AV, LV	p	0.0700	0.0081	(0.0542, 0.0858)
1b	EI	p	0.0700	0.0081	(0.0559, 0.0876)
1b	LI	p	0.0700	0.0081	(0.0553, 0.0869)
1c	AV, LV	p	0.9930	0.0026	(0.9878, 0.9982)
1c	EI	p	0.9930	0.0026	(0.9870, 0.9972)
1c	LI	p	0.9930	0.0027	(0.9865, 0.9970)
2a	AV	M	280.0	101.6	(112.8, 400.0)
2a	LV	M	279.5	101.6	(112.3, 400.0)
2a	AAV	M	280.0	104.5	(108.1, 400.0)
2a	LI	M	279.5	94.7	(123.7, 400.0)
2a	ALI	M	279.5	95.8	(121.8, 400.0)
2b	AV	M	70.0	24.4	(22.2, 117.8)
2b	LV	M	69.6	24.4	(21.8, 117.3)
2b	AAV	M	70.0	25.1	(20.8, 119.2)
2b	LI	M	69.6	24.5	(32.2, 128.2)
2b	ALI	M	69.5	25.5	(31.6, 131.5)
2c	AV, LV	M	2800	321	(2170, 3430)
2c	AAV	M	2800	330	(2152, 3448)
2c	LI	M	2800	322	(2214, 3475)
2c	ALI	M	2800	331	(2201, 3499)

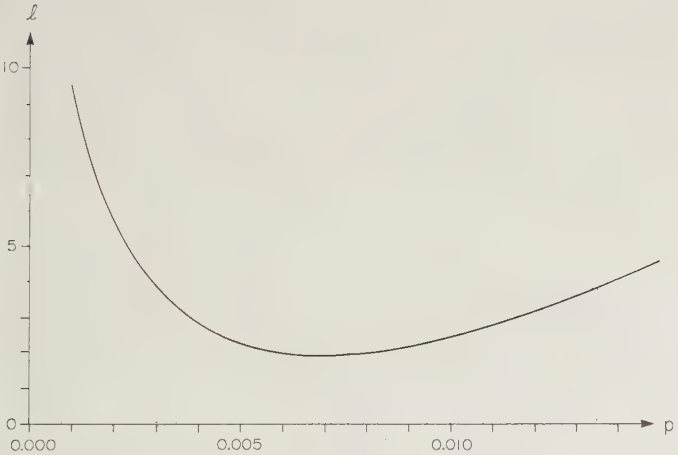


FIG. 1. Plot of $\ell(p)$ vs. p for example 1a (Table 4). The minimum point on the curve determines the likelihood estimate $\hat{p}$. Dotted lines indicate this point and a level 1.92 (i.e. $\chi^2(0.95, 1)/2$) units above it. Two vertical dotted lines intersect the p-axis at the end points of a 95% inference interval determined from (5.1).

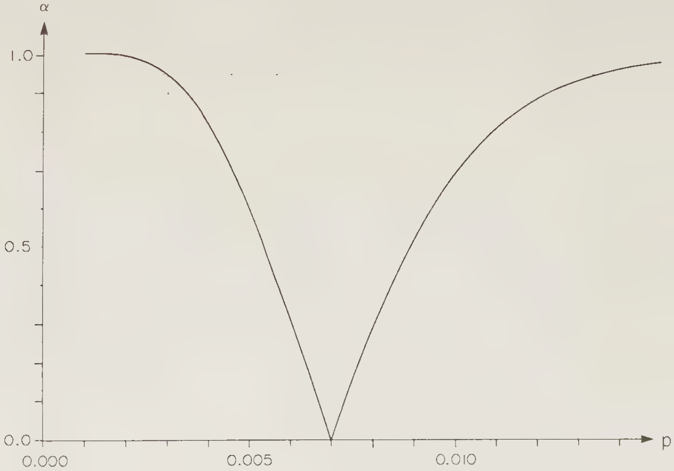


FIG. 2. Likelihood inference level $\alpha(p)$ for rejecting a value of p, as computed from (5.3) and the function $\ell(p)$ in Fig. 1. The horizontal dotted line intersects the curve at two points that determine a 95% inference interval for p, as demarcated by vertical dotted lines. In general, for any given α, the figure can be used to determine an α-level inference interval for p.

$$(5.4)\quad \theta_- = \hat{\theta} + \nu(1-\alpha)\widehat{\sigma(\hat{\theta})}$$

where $\theta = M$. Similarly, when M_- comes directly from an interval method, $\widehat{\sigma(\hat{\theta})}$ is computed using

$$(5.5)\quad \widehat{\sigma(\hat{\theta})} = \frac{\theta_- - \hat{\theta}}{\nu(1-\alpha)}.$$

In particular, $\nu(1-\alpha) = -1.645$ when $\alpha = 95\%$.

For each of the six examples, Table 5 shows that all methods lead to similar estimates $\hat{\theta}$ and $\widehat{\sigma(\hat{\theta})}$. In particular, similarities among standard errors $\widehat{\sigma(\hat{\theta})}$ indicate that all methods lead to 95% inference intervals with similar widths. By contrast, although the methods generally agree on an interval's width, they may show marked differences related to its position around the estimate $\hat{\theta}$. As noted earlier, variance methods give symmetric intervals (4.1). By contrast, Fig. 1 shows that the LI method applied to example 1a leads to asymmetry. In this case, $\ell(p)$ is relatively shallow for p above $\hat{p}$; consequently, (p_-, p_+)

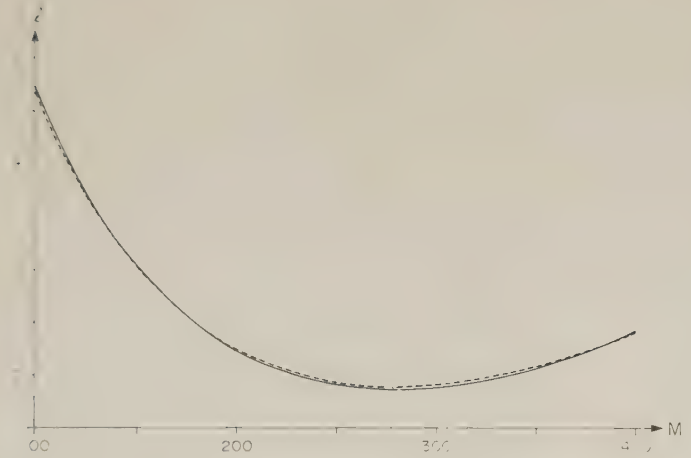


FIG. 3. Exact (solid curve) and approximate (broken curve) functions $\ell(M)$ vs. M for example 2a (Table 4). Both functions are computed from (4.11), where the exact result comes from (3.6) and the approximation from (4.15). Dotted lines indicate the process of determining a 95% inference interval from (4.14). Values $M > 400$ are not considered, since these would violate the constraint $M \leq C$.

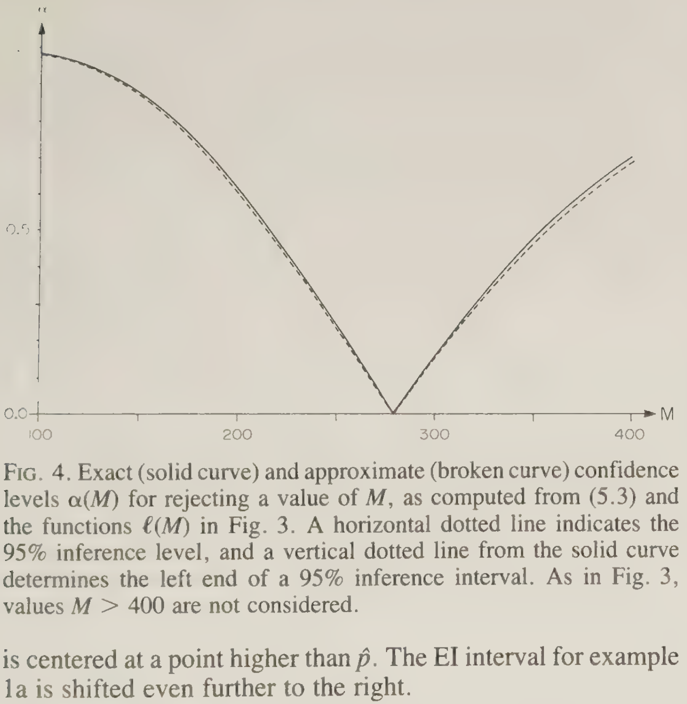


FIG. 4. Exact (solid curve) and approximate (broken curve) confidence levels $\alpha(M)$ for rejecting a value of M, as computed from (5.3) and the functions $\ell(M)$ in Fig. 3. A horizontal dotted line indicates the 95% inference level, and a vertical dotted line from the solid curve determines the left end of a 95% inference interval. As in Fig. 3, values $M > 400$ are not considered.

is centered at a point higher than $\hat{p}$. The EI interval for example 1a is shifted even further to the right.

Examples 1a and 1c illustrate a certain duality in data for the binomial distribution. Of 1000 fish, 7 are recovered and 993 are not in example 1a, while 993 are recovered and 7 are not in example 1c. If p_a and p_c denote recovery probabilities for 1a and 1c, respectively, then the following dual estimates might be anticipated:

(5.6) $\hat{p}_c = 1 - \hat{p}_a$

(5.7) $(p_{c-}, p_{c+}) = (1 - p_{a+}, 1 - p_{a-})$

(5.8) $\widehat{\sigma(\hat{p}_c)} = \widehat{\sigma(\hat{p}_a)}$.

Intuitively, the results should be self-consistent, whether one focuses on the fish recovered or not recovered. Although the AV, LV, and LI methods all conform to (5.6)–(5.8), the EI method does not. As proved in Appendix D, the EI method would satisfy (5.7) exactly if $N = 992$ in example 1c.

Examples 2a and 2c illustrate the process of adding a scale factor to the data; thus, each fish in 2a is replaced by 10 fish in 2c. As a result, the AV estimate $\hat{M}$ for 2c is exactly 10 times that for 2a. By contrast, the AV estimate $\widehat{\sigma(\hat{M})}$ is only about $\sqrt{10}$ times that for 2a. Due to this relatively small standard error, two-sided confidence intervals are appropriate for example 2c, although they are not for example 2a. The reader can verify from (4.7)–(4.8) that adding a scale factor f to C, S, and X automatically scales $\hat{M}$ by f and $\widehat{\sigma(\hat{M})}$ by an approximate factor $\sqrt{f}$. Such behaviour characterizes the Poisson distribution, which might also be used as an approximation to distributions decribed here.

6. Conclusions

The intuitive arguments in section 2 summarize my principle concerns with the use of embedded replication in mark–recovery experiments. In my view, the fundamental difficulty is described in points 4 and 5. Since embedded replicates are designed to be indistinguishable, no cause can be attributed to statistical differences (if any) that are observed among them. To extract useful conclusions from the data, it would be necessary to adopt a statistical model in which fish from different embedded groups experience different fates. Such a model would be hard to justify, given the experimental method of applying embedded tag codes. This becomes particularly apparent when contemplating a computer program to simulate data from an embedded replicate experiment. Furthermore, sections 2 and 3 of the paper provide analytic proof in two contexts that data from multiple embedded codes can equivalently be generated *after* completing an experiment with a single code.

One proposed use of embedded replication has been to estimate uncertainty in parameters obtained from CWT data. The final point in section 2 cites at least one problem with this concept. Since embedded codes are applied at the point of release, they cannot be used to measure sources of variability due to the recovery process. Thus,' calculations like (0.3) can actually be deceptive.

Since I have argued that embedded replication is not appropriate for calculating variances, I have included detailed examples in sections 4 and 5 to illustrate methods that can be used in classical experiments with single tag codes. I have examined a variety of possibilities, including recent moment methods proposed by Clark and Bernard (1987) and Newman (1990). For the examples worked here, the methods differ primarily with regard to asymmetric inference intervals (θ_-, θ_+) around the estimates $\hat{\theta}$. Using bootstrap techniques, Geiger (1990) found asymmetries similar to those obtained here with the LI method. In fact, a variant of the LI method (not developed here) could employ an equation analogous to (4.14), in which the χ^2 distribution is replaced by a distribution obtained from simulation.

Approximations sometimes provide adequate alternatives to the complex distributions inherent in realistic CWT experiments. For example, I have cited (4.15) as a possible alternative to (3.6). I have also suggested that a Poisson distribution might be appropriate in some cases. Simulations could be used to identify the range of validity for such approximations, and, after suitable testing, they might legitimately be employed in specific contexts.

True replication will, of course, continue to be a fundamental tool in designing CWT experiments. For example, the survival experiments reported by Bilton et al. (1982) illustrate the importance of replicated ponds in measuring the effects of different hatchery practices. Although embedded replication is possible mechanically, it cannot be adopted as a valid CWT technique until its proponents articulate clear and appropriate statistical models for analysis of the data.

Acknowledgements

I am grateful for advice, encouragement, and thoughtful skepticism from fellow members of the International Working Group on Mark Recovery Statistics, organized by the Pacific Salmon Commission. In particular, theoretical work by K. Newman and simulation studies by R. Comstock led me to investigate many of the issues raised here. My own struggle with this problem has been assisted by helpful discussion and spirited debate with numerous colleagues, including F. de Libero, R. Hillborn, R. Kronlund, T. Mulligan, D. Noakes, and T. Perry. Four anonymous reviewers provided thoughtful critique on an earlier draft. Figures were drafted by L. Fitzpatrick and photographed by E. Warneboldt.

References

ABRAMOWITZ, M., AND I. A. STEGUN. 1966. Handbook of mathematical functions. National Bureau of Standards Applied Mathematics Series, 55. 5th printing, with corrections. U.S. Government Printing Office, Washington, DC. 1046 p.

BILTON, H. T., D. F. ALDERDICE, AND J. T. SCHNUTE. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426–447.

CLARK, J. E., AND D. R. BERNARD. 1987. A compound multivariate binomial–hypergeometric distribution describing microwire tag recovery from commercial salmon catches in southeast Alaska. Alaska Dep. Fish Game (Juneau) Inf. Leafl. 261.

COCHRAN, W. G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, New York, NY. 428 p.

GEIGER, H. J. 1990. Parametric bootstrap confidence intervals for estimating contributions to fisheries from marked salmon populations. Am. Fish. Soc. Symp. 7: 667–676.

KENDALL, M., AND A. STUART. 1979. The advanced theory of statistics. Vol. 2: Inference and relationship. 4th ed. MacMillan Publ. Co., Inc., New York, NY. 738 p.

KUHN, B. R., L. LAPI, AND J. M. HAMER. 1988. An introduction to the Canadian database on marked Pacific salmonids. Can. Tech. Rep. Fish. Aquat. Sci. 1649: 56 p.

LAPI, L., M. HAMER, AND B. JOHNSON. 1990. Data organization and coding for a coastwide mark–recovery data system. Am. Fish. Soc. Symp. 7: 720–724.

MITTERTREINER, A., AND J. SCHNUTE. 1985. Simplex: a manual and software package for easy nonlinear estimation and interpretation in fishery research. Can. Tech. Rep. Fish. Aquat. Sci. 1384: 90 p.

MOOD, A. M., AND F. A. GRAYBILL. 1963. Introduction to the theory of statistics. 2nd ed. McGraw-Hill Book Co., Inc., New York, NY. 443 p.

NELDER, J. A., AND R. MEAD. 1965. A simplex method for function minimization. Comput. J. 7: 308–313.

NEWMAN, K. 1990. Variance estimation for stock-contribution estimates based on sample recoveries of coded-wire-tagged fish. Am. Fish. Soc. Symp. 7: 677–683.

PERRY, E. A., H. L. BLANKENSHIP, AND R. V. PALERMO. 1990. Comparison of two methods for replicating coded wire tag studies. Am. Fish. Soc. Symp. 7: 660–666.

POLLARD, J. H. 1977. A handbook of numerical and statistical techniques, with examples mainly from the life sciences. Cambridge University Press, Cambridge, U.K. 349 p.

SCHNUTE, J. 1983. A new approach to estimating populations by the removal method. Can. J. Fish. Aquat. Sci. 40: 2153–2169.

Appendix A. Proof of (3.16)

A typical term T in (3.15) has the form

$$\text{(A.1)}\quad T = 2^{-N} p^N (1-p)^{M-N} A \binom{C-N}{S-X} \bigg/ \binom{C}{S}$$

where

$$\text{(A.2)}\quad A = \binom{M}{N_1\, N_2} \binom{N_1}{X_1} \binom{N_2}{X_2} .$$

The product A can also be written in the form

$$\text{(A.3)}\quad A = \binom{M}{N} \binom{N}{X} \binom{X}{X_1} \binom{N-X}{N_1-X_1} ,$$

as can be confirmed by expressing (A.2) and (A.3) in terms of factorials.

The double sum (3.15) involves the index variables N_1 and N_2, where the sum over N_1 occurs first. Equivalently, (3.15) can be expressed as a double sum taken first over N_1 and then over N in (3.10). This gives

$$\text{(A.4)}\quad L = \sum_{N=X}^{M} \sum_{N_1=X_1}^{N-X_2} T$$

where L denotes the likelihood $L(X_1, X_2|M, p, C, S)$. The summation ranges in (A.4) result from those in (3.15), given the relationships (3.9)–(3.10).

It follows from (A.1) and (A.3) that T depends on N_1 only via the factor $\binom{N-X}{N_1-X_1}$. Furthermore, a standard identity for binomial coefficients states that

$$\text{(A.5)}\quad \sum_{N_1=X_1}^{N-X_2} \binom{N-X}{N_1-X_1} = 2^{N-X}$$

where the proof of (A.5) involves replacing the index N_1 with a new index $K = N_1 - X_1$. Combining (A.1), (A.3), (A.4), and (A.5) gives

$$\text{(A.6)}\quad L = 2^{-X} \binom{X}{X_1} \times \sum_{N=X}^{M} \binom{M}{N} p^N (1-p)^{M-N} \binom{N}{X} \binom{C-N}{S-X} \bigg/ \binom{C}{S} .$$

The result (A.6), together with the likelihood definitions (3.6) and (3.17), completes the proof of (3.16).

Appendix B. Moments in Table 3

Results in Table 3 for the binomial and hypergeometric distributions are well known (Pollard 1977, p. 100 and 119). My derivation of the B-H moments in Table 3 parallels a similar derivation by Newman (1990). The B-H variate X in (3.6) results from a compounding a binomial variate N with a hypergeometric X. From general properties of compound distributions, it follows that the expected value and variance of the B-H variate X can be computed from

$$\text{(B.1)}\quad E[X] = E_N[E[X|N]]$$

and

$$\text{(B.2)}\quad V[X] = V_N[E[X|N]] + E_N[V[X|N]],$$

respectively. In (B.1)–(B.2), $E[X|N]$ and $V[X|N]$ denote moments of the hypergeometric variate X for a given value N. Similarly, E_N and V_N denote the expected value and variance with respect to the binomial variate N.

From established results in Table 3, it follows that

(B.3) $E[X|N] = \frac{SN}{C}$

(B.4) $V[X|N] = \frac{SN(C-N)(C-S)}{C^2(C-1)}$

(B.5) $E_N[N] = Mp$

(B.6) $V_N[N] = Mp(1-p)$

(B.7) $E_N[N^2] = Mp(Mp+1-p)$.

In particular, (B.7) follows from (B.5)–(B.6) and the general result

$$E_N[N^2] = V_N[N] + (E_N[N])^2.$$

Substituting (B.3) and (B.5) into (B.1) gives the expression $E[X]$ for the B-H distribution reported in Table 3. Similarly, substituting (B.3)–(B.7) into (B.2) gives the reported expression $V[X]$. The latter calculation requires a few lines of algebra not presented here.

Appendix C. Computational Details

Likelihood functions in this paper require frequent calculation of the factorial function. Schnute (1983, p. 2168) gave an efficient formula for log(x!). His method uses Stirling's approximation when $x \geqslant 3$ and takes advantage of the relationship

$$x! = \frac{(x+3)!}{(x+3)(x+2)(x+1)}$$

when $0 \leqslant x < 3$. The method leads to rapid computation and extremely accurate results.

Calculations should be confined to a logarithmic scale as much as possible. For example, the function $\ell(p)$ from (2.1) and (4.11) should be computed as

$$\ell(p) = -\log(M!) + \log(N!) + \log[(M-N)!] \\ -N\log(p) - (M-N)\log(1-p).$$

The function $\ell(M)$ from (3.6) and (4.11) is the logarithm of a sum, so that terms within the sum must be computed on an absolute scale. For each term, first compute its logarithm and then apply the exponential function to obtain its actual value.

Mittertreiner and Schnute (1985) described computational methods for the likelihood calculations (4.12)–(4.14). In particular, the simplex method (Nelder and Mead 1965) is used for function minimization in (4.12). Derivatives in (4.13) are taken numerically.

Appendix D. Dual Results from the EI Method

Consider two examples for the binomial distribution, both of which involve the same number M of marked fish. If the number of recoveries is N_i in example i ($i = 1, 2$), suppose that

(D.1) $N_2 = M - N_1 - 1$,

so that nearly opposite numbers of fish are recovered or not recovered. Let $p_{i\pm}$ denote the end points of an α-level inference interval for example i ($i = 1, 2$) obtained via the EI method (4.9)–(4.10). Then the intervals satisfy the following relationship analogous to (5.7):

(D.2) $(p_{2-}, p_{2+}) = (1 - p_{1+}, 1-p_{1-})$.

Proof of (D.2) follows from (D.1), (4.9), (4.10), and the identify

$$F(\alpha, m, n) = \frac{1}{F(1-\alpha, n, m)}$$

for the F distribution (Abramowitz and Stegun 1966, eq. 26.6.9). In particular, the more natural assumption $N_2 = M - N_1$ does not imply (D.2) for the EI method, although it does lead to the relationship $\hat{p}_2 = 1 - \hat{p}_1$ between estimates $\hat{p}_i$ for example i ($i = 1, 2$).

Difference in the Seawater Tolerance of Anadromous and Landlocked Populations of Arctic Char (*Salvelinus alpinus*)

Magne Staurnes,[1] Trygve Sigholt,[1] and Grete Lysfjord[2]

Department of Zoology, AVH, University of Trondheim, N-7055 Dragvoll, Norway

and Odd A. Gulseth

Environmental Protection Department, The County Governor of Nordland, N-8000 Bodø, Norway

Staurnes, M., T. Sigholt, G. Lysfjord, and O. A. Gulseth. 1992. Difference in the seawater tolerance of anadromous and landlocked populations of Arctic char (*Salvelinus alpinus*). Can. J. Fish. Aquat. Sci. 49: 443–447.

The seawater tolerance of juvenile fish from an anadromous and a landlocked population of Arctic char (*Salvelinus alpinus*), reared in freshwater under a constant light regime, was compared by making repeated seawater challenge tests from one summer to the next. Fish from the landlocked population had higher mortality rates and higher blood plasma Na^+ concentrations after transfer to seawater than those from the anadromous population. The gill Na-K-ATPase activity of the landlocked fish was lower than that of the anadromous fish. For both populations, the smallest fish showed the lowest seawater tolerance, but hypoosmoregulatory ability was independent of fish size for fish larger than about 60 g. By June of the second summer, fish from the anadromous, but not those from the landlocked population, developed seawater tolerance 10 d after transfer to seawater. This increase in hypoosmoregulatory ability was accompanied by a doubling of the gill Na-K-ATPase activity.

Les auteurs ont comparé la tolérance à l'eau salée d'ombles chevaliers (*Salvelinus alpinus*) juvéniles issus d'une population anadrome et confinée aux eaux intérieures. Ils les ont élevés en eau douce dans des conditions d'éclairement continu puis les ont soumis à des essais répétés d'acclimatation à l'eau salée d'un été à l'autre. Les individus issus de la population anadrome ont présenté des taux de mortalité et des concentrations de Na^+ dans le plasma sanguin plus élevés après le transfert en eau salée que les individus issus de la population confinée aux eaux intérieures. Le niveau d'activité de la Na-K-ATPase dans les branchies de ces derniers était aussi moins élevé. Chez les deux populations, les plus petits individus ont montré le plus faible niveau d'acclimatation à l'eau salée; par contre, la capacité hypoosmorégulatoire était indépendante de la taille du poisson chez les individus de plus de 60 g de poids. Dès juin du deuxième été, les poissons issus de la population anadrome s'étaient acclimatés à l'eau salée 10 jours après leur transfert; ceci n'était pas le cas des poissons issus de la population confinée aux eaux intérieures. Cette augmentation de la capacité hypoosmorégulatoire était accompagnée d'un accroissement du double de l'activité de la Na-K-ATPase dans les branchies.

Received June 6, 1990
Accepted October 10, 1991
(JA596)

Reçu le 6 juin 1990
Accepté le 10 octobre 1991

Arctic char (*Salvelinus alpinus*) have a circumpolar distribution, with anadromous forms predominating in more northerly areas. In anadromous populations, the seaward migration usually coincides with the ice breakup of coastal rivers (Grainger 1953; Nordeng 1977). Veteran migrants normally migrate 1–2 wk before the first-time migrants (Nordeng 1977; Berg and Berg 1989). Anadromous Arctic char are not known to overwinter at sea; thus, their residence at sea lasts for only a few weeks in some areas (Johnson 1980; Gyselman 1984) to several months in other areas (Dempson and Kristofferson 1987). In addition, marine migrations are usually confined to localized areas.

Information on the development of seawater tolerance by Arctic char is limited by comparison with other salmonid species. Recently, however, the seawater tolerance of anadromous fish has been found to vary seasonally, being high in summer and low in autumn and winter (Finstad et al. 1989a; Arnesen et al. 1992). The results of these studies indicate that the anadromous Arctic char, when reared under natural photoperiod conditions, undergoes a similar, preparatory adaptation to seawater as that demonstrated for several species of *Salmo* and *Oncorhynchus* (Hoar 1988).

Within the geographical limits of anadromy, many Arctic char stocks have subsequently become isolated by the isostatic rise in land level relative to sea level, following the melting of the ice sheets at the end of the last Ice Age (Johnson 1980). Landlocked populations are also found in some boreo-alpine areas south of this limit of anadromy, which in Norway lies at about 65°N (Nordeng 1961). Even though such landlocked populations have been isolated from the sea for several thousand years, some degree of euryhalinity has also been documented for fish from these populations (Roberts 1971; Stefansson et al. 1987; Ringø et al. 1988; Finstad et al. 1989b). A direct comparison of the hypoosmoregulatory ability of Arctic char from anadromous and landlocked populations does not appear, however, to have been made. The objective of the present experiment was to make such a comparison and investigate whether such isolation from seawater of a landlocked population has had any influence on the ability to adapt to seawater conditions.

---

[1] Present address: SINTEF Applied Chemistry, Center of Aquaculture, N-7034 Trondheim, Norway.

[2] Present address: Nordland College, Fisheries Division, Box 6003, N-8016 Mørkved, Norway.

Material and Methods

Origin of Fish

First-generation hatchery-reared fish, obtained from an anadromous and from a landlocked population of Arctic char in 1983, were monitored from July 1985 to June 1986 in a hatchery in northern Norway (68°N). The anadromous population was derived from Strandvatn Lake in northern Norway (68°N). This lake lies only 5 m above sea level and is connected to the sea by a river about 0.2 km in length. The landlocked population came from Unkervatn Lake, also in northern Norway (66°N). This lake lies 310 m above sea level about 100 km from the sea. There is no population of anadromous Arctic char in the watercourse to which the lake is connected.

Experimental Design

The fish from each population (about 1600) were reared in two separate 4-m^2 plastic tanks (1.6 m^3) supplied with freshwater and were fed a commercial pelleted food ad libitum. The fish were not sorted. The tanks were placed indoors under a 24-h continuous light regime. Between the end of October and the end of April, the water temperature was 2–4°C. During May and June, the temperature rose to 10–12°C.

The seawater tolerance was tested on 20 July 1985 and on 21 January, 23 March, 1 May, and 2 June 1986 by transferring fish directly from freshwater into 4-m^2 plastic tanks (1.6 m^3) continuously supplied with seawater. In July 1985 the tolerance was tested by recording the mortality rate for 18 d, using 20 fish from each of the anadromous and landlocked populations. In 1986, fish kept 1, 3 and 10 d in seawater were sampled for measurement of gill Na-K-ATPase activity, blood plasma Na^+ concentration, and muscle water content, and the mortality rates during the seawater period were recorded. The 10-d tests were carried out separately from the 1- to 3-d tests. About 25 fish from each population were used in the 1- to 3-d tests. In the 10-d tests, 13 anadromous fish were tested in May and 10 in June; otherwise the number of fish from each population was 20–27. Except for the 10-d test in May, when all surviving fish were sampled, nine fish were sampled for physiological investigation. In January, the water was oxygenated between the second and the third days of the tests due to a failure in the seawater supply. Because of this failure, the 10-d test at this time was carried out in a neighbouring hatchery, in which the salinity of the seawater was 27‰. In all other tests the salinity was 33‰. The seawater temperature in July 1985 was 11°C, between January and May 1986 was 5–6°C, and in June 1986 was 8.5°C.

In all tests, the size of the fish from the two populations was the same. In July 1985 the weight and length of the fish tested were 20–40 g and 13–17 cm, respectively. In the tests carried out in 1986 the fish weighed 50–170 g and had a length of 19–26 cm. In June, additional groups of 12 fish of smaller size (20–45 g, 14–18 cm) from both populations were transferred to seawater for 1 d, and the fish were thereafter killed for analysis of blood plasma Na^+ concentration.

On 21 January, 23 March, 1 May and 2 June 1986, nine fish from each population (weight 50–170 g, length 19–26 cm) kept in freshwater were sampled for similar physiological analyses as the seawater-exposed fish.

Sampling Procedure, Analyses, and Statistics

The fish sampled for physiological analyses were killed by a blow to the head, their length and weight were determined, and blood samples were collected from the caudal vessels into heparinized tubes by cutting the caudal fin. Blood samples were centrifuged and plasma frozen for determination of Na^+ concentration. Gill arches were dissected out, carefully dried with soft paper, and the filaments were cut free. About 0.1 g of the gill tissue was placed in 1.0 mL of buffer solution (Zaugg 1982) and immediately frozen in liquid nitrogen for subsequent determination of Na-K-ATPase activity. A piece of white epaxial muscle was dissected out below the dorsal fin, wrapped in aluminium foil and frozen for later determination of its water content.

All the inspected fish from the landlocked population were immature whereas a large proportion of those from the anadromous population were found to be maturing. Only the results for immature fish have been used in the present study.

Blood plasma Na^+ concentration was assayed using a Perkin Elmer 300 atomic absorption spectrophotometer. Water content of the muscle tissue samples was determined as described by Lutz (1972). Gill Na-K-ATPase activity was assayed as described by Finstad et al. (1989a) and is expressed as micromoles of P_i per milligram of protein per hour.

Wilcoxon's two-tailed test was used for comparison of sample means, and a significance level of $P < 0.05$ was chosen.

Results

In the seawater challenge test carried out for 18 d in July 1985, about 20% of the fish from the anadromous and 70% of those from the landlocked population died, almost all during the first 8 d (Fig. 1). In the tests in 1986, mortality was only recorded from the landlocked fish in the 10-d tests in May (3 of 20 fish) and June (5 of 25 fish). In both populations, no differences in physiological parameters were found between the fish sampled in January, March, and May, and the results were pooled for this period (except results from the 10-d test in January which were excluded because of the lower salinity of this test). The size of the fish sampled for physiological analyses was about the same on all sampling dates and did not differ between the two populations (mean weights 90–109 g and mean lengths 20.9–23.4 cm).

In all the seawater challenge tests, the mean values for blood plasma Na^+ concentration were significantly higher than when fish were in freshwater, and all the mean values for the muscle water content were significantly lower except that recorded for the anadromous fish in the 10-d test in June (Fig. 2). In all tests, the landlocked fish had a significantly higher mean plasma Na^+ concentration than the anadromous fish, and the landlocked fish also had a tendency to show a lower muscle water content. The mean values for both parameters when fish were in freshwater were about the same for anadromous and landlocked fish and remained unchanged in all months tested.

While fish were in freshwater, the mean values for gill Na-K-ATPase activity of the anadromous population were significantly higher than those for the landlocked population (Fig. 2). Values for both populations when in freshwater remained unchanged in all months tested. In the tests carried out from

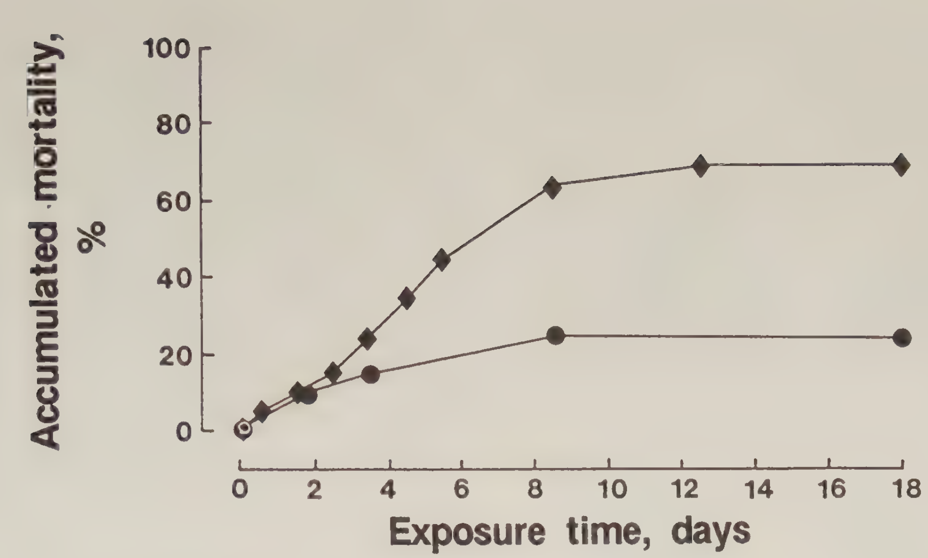


FIG. 1. Accumulated mortality of Arctic char from an anadromous population (●) and a landlocked population (◆) after transfer to seawater (salinity 33‰) in July 1985.

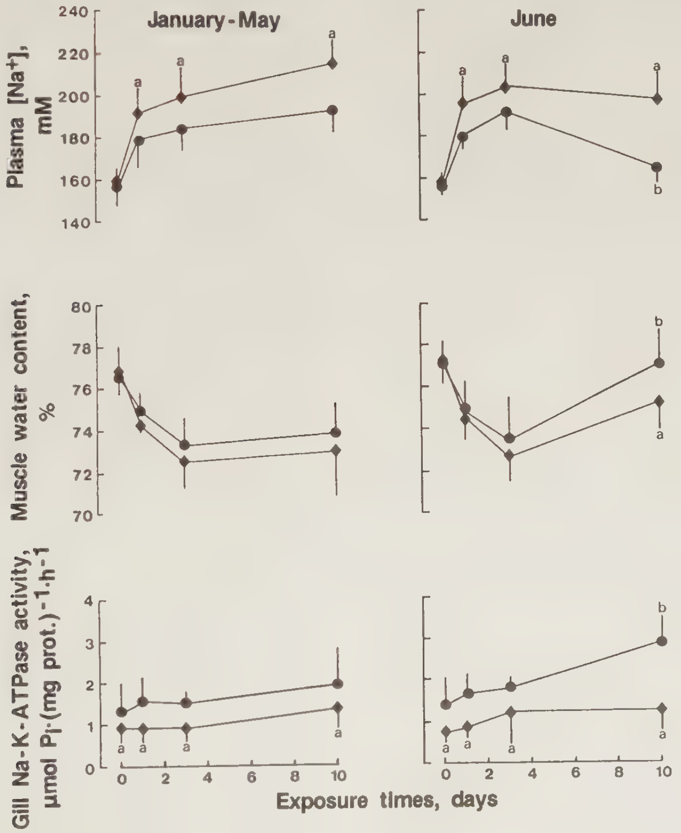


FIG. 2. Blood plasma Na^+ concentration, water content of epaxial muscle tissue, and gill Na-K-ATPase activity of Arctic char from an anadromous population (●) and a landlocked population (◆) reared in freshwater (day 0) and after 1, 3, and 10 d of exposure to seawater (salinity 33‰) in January, March, and May 1986 (N = 14–26) and in June 1986 (N = 7–9). Values are means ±SD (a, anadromous and landlocked values significantly different at this exposure time; b, values in June significantly different from the corresponding values in January–May).

January to May, the mean gill Na-K-ATPase activities for the fish challenged for 1, 3, and 10 d in seawater were not significantly different from the mean activities for the fish in freshwater. In June, however, the activity for the anadromous fish was significantly higher after 10 d in seawater than that in freshwater (Fig. 2). In this test, the anadromous fish also had a mean plasma Na^+ concentration only 10 mM higher than that recorded simultaneously for the fish kept in freshwater and a

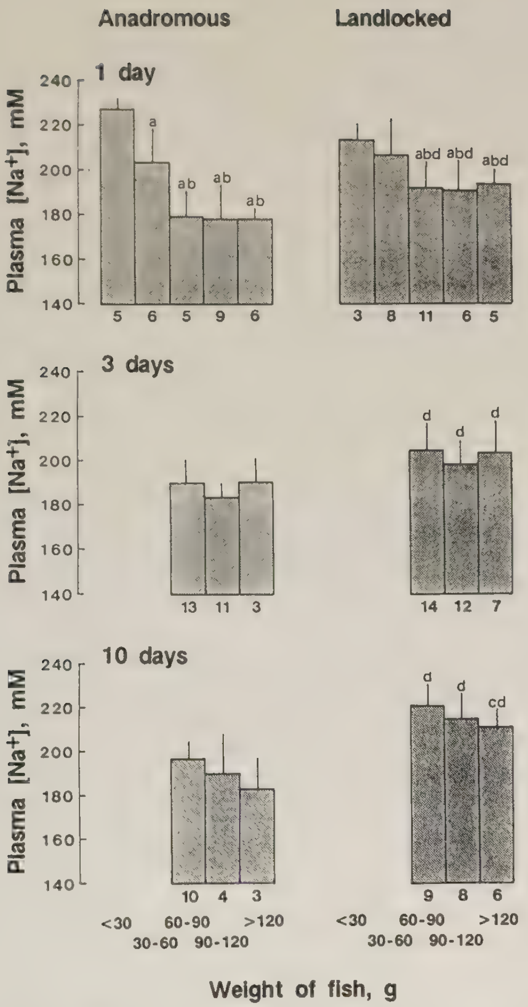


FIG. 3. Blood plasma Na^+ concentration of different weight classes of Arctic char from an anadromous and a landlocked population 1, 3, and 10 d after transfer to seawater (salinity 33‰). Results for the 10-d seawater exposure in January and June are excluded (see text for explanation). Values are the pooled means ± SD for all sampling dates with *N* given below the bars (a, b, and c, values significantly different from the corresponding values of the weight class 0–30 g (a), 30–60 g (b), and 60–90 g (c); d, values for the landlocked population significantly different from those of same weight class of the anadromous population).

muscle water content that did not differ from the mean freshwater value (Fig. 2). The results for the landlocked population, however, did not differ from those recorded in the earlier tests.

For both populations, fish weighing less than about 60 g (corresponding to a length of 18–19 cm) had significantly higher mean blood plasma Na^+ concentration after 1 d in seawater than those larger than about 60 g (Fig. 3). For larger fish, the mean plasma Na^+ concentrations for both populations did not differ with fish size. For the 10-d tests, the results from the test in January were excluded because of lower seawater salinity in this test, and those from the test in June were excluded because of the better hypoosmoregulatory ability of the anadromous fish at this time. Gill Na-K-ATPase activity was not correlated with fish size for fish from either population.

Discussion

Fish from the landlocked population of Arctic char showed a much lower seawater tolerance than those from the anadromous population, as judged from the higher mortality rate and the much higher mean blood plasma Na^+ concentration following transfer to seawater. For both the investigated populations, there was an increase in hypoosmoregulatory ability with increasing size similar to that previously reported for several other salmonids (Wilder 1952; Parry 1958, 1960; Houston 1961; Conte and Wagner 1965; Wagner et al. 1969; Wagner 1974; McCormick and Naiman 1984; Johnston and Cheverie 1985; Duston and Saunders 1990). However, the plasma Na^+ concentration after seawater exposure did not decrease with increasing body size for fish larger than about 60 g (18 cm). Similarly, Duston and Saunders (1990) reported no further decrease in plasma osmolality for Atlantic salmon (*Salmo salar*) larger than 60 g when exposed for 1 d to 29‰ seawater.

Although none of the anadromous fish died in the seawater challenge tests in 1986, the great increase in their plasma Na^+ concentration and the decrease in their muscle water content showed that they too suffered a marked osmoregulatory stress following their transfer to seawater. In June, however, the plasma Na^+ concentration and muscle water content values recorded after 10 d in seawater approached those before the challenge. This increase in hypoosmoregulatory ability was associated with a marked increase in the gill activity of Na-K-ATPase, which is an important enzyme in the salt extrusion mechanism of the teleost gill in seawater (e.g. Payan et al. 1984). Thus, in the June test the anadromous Arctic char, in contrast with the landlocked char, were able to develop seawater tolerance when in seawater but showed no preparatory increase in gill Na-K-ATPase activity and seawater tolerance when in freshwater. The gill Na-K-ATPase activity of fish in freshwater was very similar to that found by Finstad et al. (1989a) during winter for fish from another stock of anadromous Arctic char. When reared under natural photoperiod, anadromous Arctic char increase gill Na-K-ATPase activity and preadapt to seawater during the spring (Finstad et al. 1989a; Arnesen et al. 1992), and therefore the lack of preadaptation in the present experiment was probably due to the use of a continuous light regime.

In contrast with the anadromous fish, those from the landlocked population lacked the ability to induce an increase in their gill Na-K-ATPase activity in the seawater challenge test carried out in June 1986, and the hypoosmoregulatory ability of these fish was poor. The freshwater activity level was also lower than that for the anadromous fish. The enzyme activity and hypoosmoregulatory ability of the landlocked fish were similar to those recorded for mature individuals of the anadromous population (M. Staurnes, unpubl. data).

The results from other studies comparing the seawater tolerance of fish from anadromous and nonanadromous populations of salmonids are divergent. McCormick et al. (1985) reported no difference in the hypoosmoregulatory ability of brook trout (*Salvelinus fontinalis*) from an anadromous and a nonanadromous population. For landlocked populations of Atlantic salmon, fish from some populations show preparatory increase in gill Na-K-ATPase activity and hypoosmoregulatory ability during spring (Chernitskiy and Loenko 1983; Koch 1983; Staurnes et al. 1992), but fish from others do not (Burton and Idler 1984; Birt and Green 1986). The results from the study of Barbour and Garside (1983) indicate an incomplete parr–smolt transformation of fish from a landlocked population of Atlantic salmon when compared with fish from an anadromous population. Recently, anadromous sockeye salmon (*Oncorhynchus nerka*) have been reported to have a better seawater adaptability than nonanadromous kokanee (Foote et al. 1989). Some degree of euryhalinity has previously been documented for fish from landlocked Arctic char populations in the British Isles (Roberts 1971) and in Norway (Stefansson et al. 1987; Ringø et al. 1988; Finstad et al. 1989b). In full-strength seawater, however, the hypoosmoregulatory ability of fish from these landlocked populations was poorer than that of fish from the anadromous Arctic char populations (Fig. 2; Finstad et al. 1989a), even after a gradual adaptation to brackish water (Roberts 1971; Finstad et al. 1989b). Some differences in seawater tolerance have also been reported between anadromous stocks (Delabbio et al. 1990), and such differences may also occur between landlocked populations. The present information for Arctic char indicates, however, that seawater adaptability of anadromous populations is better than that of landlocked populations.

Acknowledgements

We thank Ove Johansen, Norwegian Water Research and Energy Administration, for providing facilities for the experiment. The experiment was financially supported by a grant from the Norwegian Research Council for Science and the Humanities to Magne Staurnes and by a grant from the Norwegian Fisheries Research Council to Trygve Sigholt.

References

ARNESEN, A. M., M. HALVORSEN, AND K. J. NILSSEN. 1992. Development of hypoosmoregulatory capacity in Arctic char (*Salvelinus alpinus*) reared under either continuous light or natural photoperiod. Can. J. Fish. Aquat. Sci. 49: 229–237.

BARBOUR, S. E., AND T. GARSIDE. 1983. Some physiologic distinctions between freshwater and diadromous forms of the Atlantic salmon, *Salmo salar* L. Can. J. Zool. 61: 1165–1170.

BERG, O. K., AND M. BERG. 1989. Sea growth and time of migration of anadromous Arctic char (*Salvelinus alpinus*) from the Vardnes River, in northern Norway. Can. J. Fish. Aquat. Sci. 46: 955–960.

BIRT, T. P., AND J. M. GREEN. 1986. Parr–smolt transformation in female and sexually mature male anadromous and non-anadromous Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 43: 680–686.

BURTON, M. P., AND D. R. IDLER. 1984. Can Newfoundland landlocked salmon, *Salmo salar* L., adapt to sea water? J. Fish Biol. 24: 59–64.

CHERNITSKIY, A. G., AND A. A. LOENKO. 1983. The osmoregulatory system and possible ways of differentiation in ecological forms of Atlantic salmon, *Salmo salar* (Salmonidae). J. Ichthyol. 23: 84–94.

CONTE, F. P., AND H. H. WAGNER. 1965. Development of osmotic and ionic regulation in juvenile steelhead trout, *Salmo gairdneri*. Comp. Biochem. Physiol. 14: 603–624.

DELABBIO, J. L., B. D. GLEBE, AND A. SREEDHARAN. 1990. Variation in growth and survival between two anadromous strains of Canadian Arctic char during long-term saltwater rearing. Aquaculture 85: 259–270.

DEMPSON, J. B., AND A. H. KRISTOFFERSON. 1987. Spatial and temporal aspects of the ocean migration of anadromous Arctic char. Am. Fish. Soc. Symp. 1: 340–357.

DUSTON, J., AND R. L. SAUNDERS. 1990. The entrainment role of photoperiod on hypoosmoregulatory and growth-related aspects of smolting in Atlantic salmon (*Salmo salar*). Can. J. Zool. 68: 707–715.

FINSTAD, B., K. J. NILSSEN, AND A. M. ARNESEN. 1989a. Seasonal changes in the seawater tolerance of Arctic charr (*Salvelinus alpinus*). J. Comp. Physiol. B. 159: 371–378.

FINSTAD, B., K. J. NILSSEN, AND O. A. GULSETH. 1989b. Seawater tolerance in freshwater-resident Arctic charr (*Salvelinus alpinus*). Comp. Biochem. Physiol. 92A: 599–600.

FOOTE, C. J., C. C. WOOD, W. C. CLARKE, AND J. BLACKBURN. 1989. The saltwater adaptability of sympatric anadromous and non-anadromous sockeye salmon and their "hybrids." Aquaculture 82: 377.

GRAINGER, E. H. 1953. On the age, growth, migration, reproductive potential and feeding habits of the Arctic char (*Salvelinus alpinus*) of the Frobisher Bay, Baffin Island. J. Fish. Res. Board Can. 10: 326–370.

GYSELMAN, E. C. 1984. The seasonal movements of anadromous Arctic charr at Nauyuk Lake, Northwest Territories, Canada, p. 575–578. *In* L. Johnson and B. L. Burns [ed.] Biology of the Arctic charr: Proceedings of the International Symposium on Arctic Charr. University of Manitoba Press, Winnipeg, Man.

HOAR, W. S. 1988. The physiology of smolting salmonids, p. 275–343. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology: the physiology of developing fish. Vol. XIB. Academic Press, New York, NY.

HOUSTON, A. H. 1961. Influence of size upon the adaptation of steelhead trout (*Salmo gairdneri*) and chum salmon (*Oncorhynchus keta*) to sea water. J. Fish. Res. Board Can. 18: 401–415.

JOHNSON, L. 1980. The Arctic char, *Salvelinus alpinus*, p. 15–98. *In* E. K. Balon [ed.] Charrs. Salmonid fishes of the genus *Salvelinus*. Vol. 1. Dr. W. Junk bv Publishers, The Hague, The Netherlands.

JOHNSTON, C. E., AND J. C. CHEVERIE. 1985. Comparative analysis of ionoregulation in rainbow trout (*Salmo gairdneri*) of different sizes following rapid and slow salinity adaptation. Can. J. Fish. Aquat. Sci. 42: 1994–2003.

KOCH, H. J. A. E. 1983. Régulation minérale et hémoglobines chez quelques saumons (*Salmo salar* L.) dulcaquicoles. Ann. Soc. R. Zool. Belg. T 113 (Suppl. 1): 259–260.

LUTZ, P. L. 1972. Extracellular spaces and the composition of various tissues of perch. Comp. Biochem. Physiol. 41A: 77–88.

MCCORMICK, S. D., AND R. J. NAIMAN. 1984. Osmoregulation in the brook trout, *Salvelinus fontinalis* — II. Effects of size, age and photoperiod on seawater survival and ionic regulation. Comp. Biochem. Physiol. 79A: 17–28.

MCCORMICK, S. D., R. J. NAIMAN, AND E. T. MONTGOMERY. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 42: 529–538.

NORDENG, H. 1961. On the biology of the char (*Salvelinus alpinus* L.) in Salangen, North Norway. 1. Age and spawning frequency determined from scales and otoliths. Nytt Mag. Zool. 10: 67–123.

1977. A pheromone hypothesis for the homeward migration in anadromous salmonids. Oikos 28: 155–159.

PARRY, G. 1958. Size and osmoregulation in salmonid fishes. Nature (Lond.) 181: 1218–1219.

1960. The development of salinity tolerance in the salmon. J. Exp. Biol. 37: 425–434.

PAYAN, P., J. P. GIRARD, AND N. MAYER-GOSTANT. 1984. Branchial ion movements in teleosts: the roles of respiratory and chloride cells, p. 39–63. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology: gills, ion and water transfer. Vol. XB. Academic Press, New York, NY.

RINGØ, E., R. KRISTOFFERSEN, AND B. NILSEN. 1988. Wild and hatchery-reared landlocked Arctic charr, *Salvelinus alpinus* (L.), from Lake Takvatn, reared in fresh and sea water. Content of free amino acids and ninhydrin-positive substances. Aquaculture 74: 359–367.

ROBERTS, R. A. 1971. Preliminary observations on the ionic regulation of the Arctic char *Salvelinus alpinus*. J. Exp. Biol. 55: 213–222.

STAURNES, M., G. LYSFJORD, AND O. K. BERG. 1992. Parr–smolt transformation of a nonanadromous population of Atlantic salmon (*Salmo salar*). Can. J. Zool. 70. (In press)

STEFANSSON, S., T. J. HANSEN, AND J. C. HOLM. 1987. Seawater adaptability of two strains of Arctic char (*Salvelinus alpinus*) reared under different light regimes. Int. Counc. Explor. Sea C.M. 1978/F:37: 16 p.

WAGNER, H. H. 1974. Seawater adaptation independent of photoperiod in steelhead trout (*Salmo gairdneri*). Can. J. Zool. 52: 805–812.

WAGNER, H. H., F. P. CONTE, AND J. F. FESSLER. 1969. Development of osmotic and ionic regulation in two races of chinook salmon, *Oncorhynchus tshawytscha*. Comp. Biochem. Physiol. 29: 325–341.

WILDER, D. G. 1952. A comparative study of anadromous populations of brook trout (*Salvelinus fontinalis* (Mitchill)). J. Fish. Res. Board Can. 9: 169–203.

ZAUGG, W. S. 1982. A simplified preparation for adenosine triphosphatase determination in gill tissue. Can. J. Fish. Aquat. Sci. 39: 215–217.

Annual Variations in Rheotactic Behaviour and Seawater Adaptability in Landlocked Arctic Char (*Salvelinus alpinus*)

Monika Schmitz

Department of Aquaculture, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden

Schmitz, M. 1992. Annual variations in rheotactic behaviour and seawater adaptability in landlocked Arctic char (*Salvelinus alpinus*). Can. J. Fish. Aquat. Sci. 49: 448–452.

The existence of basic smoltification characteristics, measured by means of seasonal changes in rheotactic behaviour and seawater adaptability, was studied from February to November in 1- and 2-yr-old landlocked Arctic char (*Salvelinus alpinus*). Up- and downstream directed movements were monitored in an annular stream tank at a water velocity of 0.2 m/s. A 48-h seawater challenge test using 25‰ seawater was performed at monthly intervals throughout the year to assess seawater adaptability. The 1-yr-old char displayed mainly nondirectional behaviour during spring, but from August onwards the movements were predominantly against the current. Seawater performance improved slightly in this group in May and June. The 2-yr-old char progressively developed a downstream behaviour and exhibited an increased seawater adaptability during spring and early summer. In late August, a marked reversal in rheotactic behaviour occurred, followed by a rapid decrease in seawater tolerance. The results demonstrate that seasonal changes in seawater adaptability and changes in migratory behaviour which were directionally consistent with smolting still exist in a population of Arctic char that has been landlocked for about 6000 yr.

L'auteur a étudié les caractéristiques fondamentales de la smoltification chez des ombles chevaliers (*Salvelinus alpinus*) landlockés de 1 et 2 ans, caractéristiques quantifiées de février à novembre grâce aux variations saisonnières de la rhéotaxie et de la capacité d'acclimatation à l'eau salée. Les déplacements vers l'amont et vers l'aval ont été surveillés dans un bassin circulaire où la vitesse du courant s'élevait à 0,2 m/s. Un essai d'acclimatation de 48 h à de l'eau salée de 25‰ a été effectué à chaque mois afin d'évaluer la capacité d'adaptation à l'eau salée. Les ombles d'un an ont généralement montré un comportement erratique au printemps, mais d'août jusqu'à la fin de l'expérience, ils se sont surtout déplaçés à contre-courant. Leur capacité d'adaptation à l'eau salée s'est quelque peu améliorée en mai et juin. Dans le cas des ombles de deux ans, ils se sont progressivement orientés vers l'aval et ont montré une plus grande capacité d'adaptation à l'eau salée au printemps et au début de l'été. À la fin d'août, une inversion marquée de la rhéotaxie a eu lieu, suivie d'une baisse rapide de la tolérance à l'eau salée. Les résultats obtenus montrent que les variations saisonnières de la capacité d'adaptation à l'eau salée et les changements du comportement migratoire directionnel correspondant à la smoltification existent encore chez une population d'omble chevalier landlockée depuis environ 6 000 ans.

Received March 27, 1991
Accepted October 10, 1991
(JA972)

Reçu le 27 mars 1991
Accepté le 10 octobre 1991

Prior to seaward migration, many salmonids undergo a transformation from a freshwater parr to a migrating smolt. This transformation is regarded as a developmental process and consists of various morphological, behavioural, and physiological changes (McCormick and Saunders 1987; Hoar 1988). The parr–smolt transformation in migrating species, particularly Pacific salmon (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*), has been studied extensively in recent years (see Hoar 1988 for review). However, little is known about these processes in species of the salmonid genus *Salvelinus*, which display a lower degree of anadromy compared with other salmonids (Rounsefell 1958; Hoar 1976).

The Arctic char (*Salvelinus alpinus*) has a circumpolar distribution (Johnson 1980). Most of the populations reside in freshwater, and anadromous forms are largely restricted to the northern part of its range (Johnson 1980). Anadromous migrations in Arctic char are characterized by spring emigrations followed by a short intensive feeding period of 1–4 mo in the sea (Mathisen and Berg 1968; Nordeng 1968; Johnson 1980). In contrast with most species of the more specialized genus *Oncorhynchus*, which undertake one single seasonal seaward migration during their lifetime, Arctic char exhibit repeated movements into seawater. In northern Norway the char spend 3–7 yr in freshwater before migrating to the sea for the first time (Nordeng 1968). Repeat migrants include both adults and juveniles (Johnson 1980).

In a recent review, McCormick and Saunders (1987) predicted that preparatory physiological adaptations for seawater entry, entailing ontogenetic differentiation, would occur in species which make one single seawater migration during their lifetime. Conversely, species which make repeated seawater entries may rely more heavily on induction by external salinity of a perpetual hypoosmoregulatory capacity. McCormick and Naiman (1984) and McCormick et al. (1985) demonstrated that physiological changes associated with parr–smolt transformation as characterized by seasonally increased seawater tolerance were undeveloped in anadromous brook trout (*Salvelinus fontinalis*). However, anadromous Arctic char display a better seawater adaptability in June compared with September and February (Finstad et al. 1989a).

The present paper tests whether a landlocked population of Arctic char develops behavioural and physiological changes

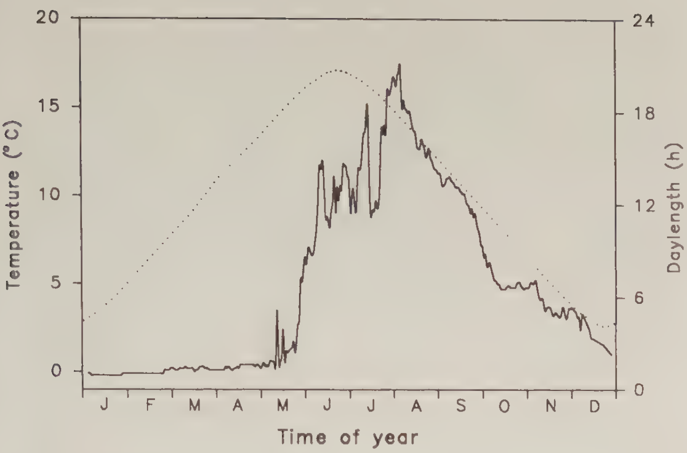


FIG. 1. Changes in daylength (dotted line) and water temperature (solid line) during the experiment.

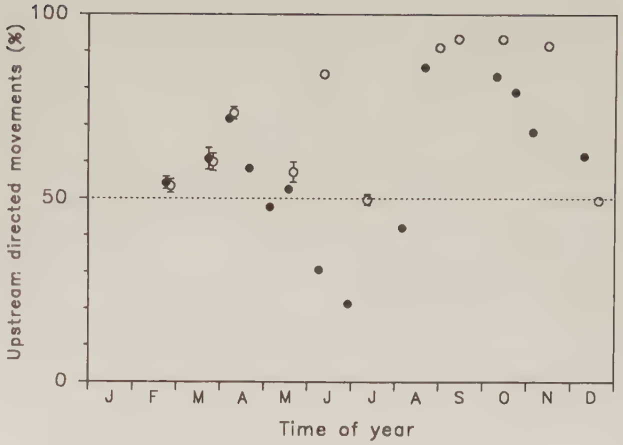


FIG. 2. Seasonal changes in rheotactic behaviour in 1-yr-old (open symbols) and 2-yr-old Arctic char (solid symbols). Rheotactic behaviour is expressed as percentage of upstream-directed movements over a 10-d period based on the total score of five fish. Error bars indicate 95% confidence limits; where not shown the limits lie within the symbols. The data of the 1-yr-old char are from Linnér et al. (1990).

typically associated with the parr–smolt transformation. Annual variations in rheotactic behaviour and seawater adaptability have been studied and the possible role of age on the development of these behavioural and physiological patterns was examined.

Material and Methods

One- and two-year-old Arctic char of a stock derived from Lake Hornavan, northern Sweden, were used in this experiment. The eggs were hatched in 1984 and in 1985, respectively, and taken to the Umeå Marine Research Centre, Norrby (63°35′N, 19°50′E). At the laboratory, fish were raised in 4-m^2 tanks, supplied with brackish water (3–5‰) at ambient temperature and under natural photoperiod. The daylength increased from a low in winter of about 4.5 h to about 21 h in mid-June (Fig. 1). During this study the water temperature was about 0.3°C until the beginning of May and rose quickly reaching a maximum of approximately 16°C during mid-August (Fig. 1). The fish were fed ad libitum with commercial dry food (Ewos) during the daytime using automatic feeders. The mean lengths of the 1- and 2-yr-old char at the start and end of the experiment were 13.9/20.7 cm and 23.7/32.9 cm, respectively.

Rheotactic behaviour was measured in the 2-yr-old fish and compared with data from 1-yr-old char of the same strain studied previously under similar experimental conditions (Linnér et al. 1990). Measurements were carried out in an annular stream tank with a diameter of 140 cm and a water depth of 30 cm. One half of the tank was narrowed to a 15-cm-wide channel, and the other was smoothly widened to 55 cm. The tank was supplied with natural brackish water (3–5‰) at ambient water temperature. A filter pump (Eheim) was placed into the tank to create a constant water current of about 0.2 m/s. The direction of the swimming movements was measured by analysing the interceptions of two infrared light beams placed at the narrowest part of the tank. The order in which the infrared light beams were crossed by a passing fish indicated the direction of movement (Lundqvist and Eriksson 1985). The number of up- and downstream movements per hour was registered on an Elmeg time printer. Rheotactic behaviour was monitored from February until December. Five fish of equal size were transferred to the tank and allowed to acclimate to the tank conditions for 2 d before starting the recordings. After a recording period of 10 d the fish were replaced by a new group. Fish were not fed during the tests.

Seawater adaptability (SWA) was assessed in 1- and 2-yr-old Arctic char using a modified seawater challenge test (Blackburn and Clarke 1987). The period of seawater exposure was extended to 48 h, since previous studies showed that the plasma ion levels in Arctic char reached constant levels after 2 d in 25‰ seawater (M. Schmitz, unpubl. data). The tests were carried out at monthly intervals from mid-February until mid-November. The 1-yr-old char could not be tested in November because of a furunculosis infection. Twelve fish from both age-groups were randomly selected from the holding tank and transferred directly to a 250-L tank of 25‰ artificial seawater (HW-Marinemix, Germany), which was aerated and stirred with a circulating pump. The water temperature was kept close to that of the holding tanks by placing the test aquarium in a tank containing flowing water at ambient temperature. After 48 h the fish were removed and anaesthetized using 2-phenoxyethanol (0.05% in seawater). For all sampled fish, fork length was measured to the nearest 0.1 cm, the fish were weighed to the nearest 0.1 g, and sex was later recorded. The fish were wiped dry and their tails cut off. Blood from the dorsal aorta was collected in ammonium heparinized hematocrit tubes and centrifuged for 5 min at 5500 rpm. The plasma was removed and stored at −25°C until analysis. Blood samples of eight untreated control fish of both age-groups were collected at the same time. Plasma sodium and magnesium levels were measured by atomic absorption spectrophotometry.

For statistical analysis, rheotactic behaviour was expressed as percentage of upstream-directed movements over a 10-d period. The calculations were based on the total score of all five fish, since the contribution of the individual fish to the total score was not known. To estimate whether there was a preference for up- or downstream movements, a two-tailed binomial test was used. The null hypothesis that there was no preference for up- or downstream movements was rejected when the 95% confidence limits of the observed proportions did not include 0.5. The statistical significance of physiological differences between the two age-groups was determined by using a two-way ANOVA. Student's *t*-test was used to estimate the differences among means of the two age-groups at any time.

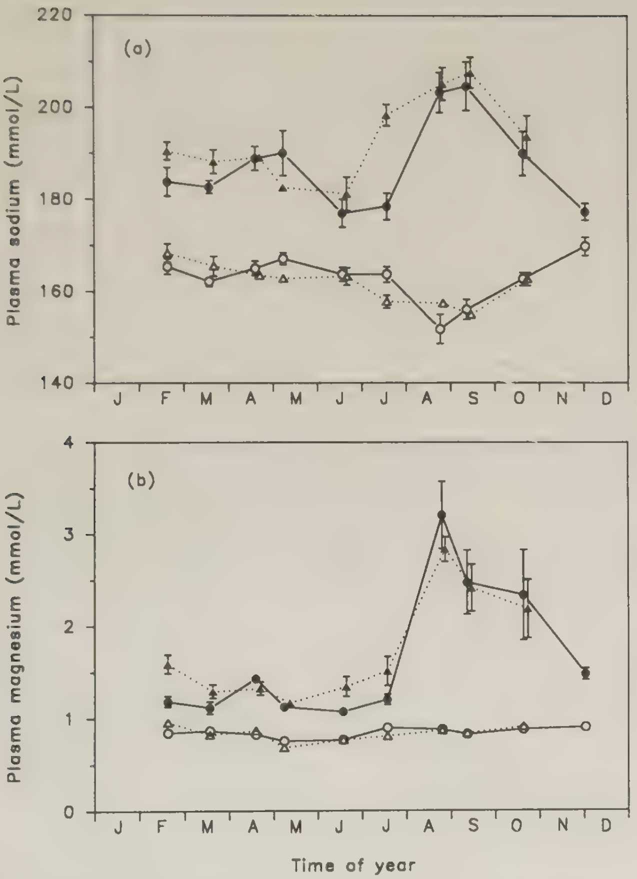


FIG. 3. Seasonal changes in (a) plasma sodium concentration and (b) plasma magnesium concentration (± SE) in 1-yr-old (triangles) and 2-yr-old Arctic char (circles). The solid symbols represent the plasma level after a 48-h seawater challenge test in 25‰ salt water. The open symbols show the values of the controls.

Differences within each group over time were determined with a one-way ANOVA and differences among means using the Tukey HSD method. The Systat statistical package (Wilkinson 1988) was used for all statistical analyses.

Results

Rheotactic behaviour in both age-groups changed over time, but there were marked differences in the swimming direction between the two groups (Fig. 2). From February to August the 1-yr-old char showed a slight preference for moving upstream, although in April and June, upstream movements were pronounced. The 2-yr-old char showed a similar pattern of upstream movement from mid-February until late April. This was followed by a period in May when movements were directed equally up- and downstream. In early June, rheotactic behaviour changed and the fish showed a clear preference for swimming with the current. This behavioural pattern was still more pronounced in late June and early July when about 80% of the movements were downstream directed. In the beginning of August the preference for downstream movements decreased. A marked change in the swimming direction was apparent in late August when about 86% of movement was against the current. At the same time the 1-yr-old char also showed an abrupt increase in the proportion of upstream-directed movements. The distinct upstream behaviour was observed in this group until the beginning of November. In the older fish, a gradual decrease occurred during late October. In December, both age-groups showed only a weak preference for upstream movements.

SWA after challenge in seawater varied considerably in both age-groups throughout the year ($p < 0.001$). The ability to regulate plasma sodium by the 1-yr-old char was poor until late April (Fig. 3a) but improved slightly during May and June. However, in July the seawater tolerance decreased markedly, as indicated by a significant increase in the sodium values from 181.2 to 198.4 mmol/L ($p < 0.002$). SWA remained poor during August and September, but improved gradually in late autumn. The 2-yr-old char displayed a similar seasonal pattern in hypoosmoregulatory ability (Fig. 3a). The plasma levels in February and March were slightly lower compared with the younger fish. An ANCOVA, using the body size as a covariate, however, revealed that these differences were due to differences in length and not in age. During June and July, SWA increased steadily ($p < 0.05$), followed by a considerable loss in seawater tolerance in late August ($p < 0.001$). The changes in the ability to regulate plasma sodium levels occurred in this group 1 mo later, and the absolute changes were greater compared with the younger fish.

The plasma magnesium concentrations after seawater challenge for the 1- and 2-yr-old char (Fig. 3b) did not show any significant changes from February until July. The magnesium values of the 1-yr-old char (Fig. 3b) tended to be higher throughout the entire spring, except for the April test. Significant differences were present in February and June ($p < 0.05$). In August the ability to regulate plasma magnesium decreased significantly ($p < 0.001$) in both age-groups. During September and October the plasma magnesium concentrations steadily declined and reached a level of 1.48 mmol/L for the 2-yr-old char in December. This value was significantly lower ($p < 0.001$) than the August value. During the entire period of investigation the plasma sodium and magnesium levels after challenge in seawater were significantly higher in both age-groups than in the untreated control groups.

Differences in SWA between males and females could not be observed in any of the seawater challenge tests. While the 1-yr-old char consisted only of immature fish, a few of the 2-yr-old char reached maturation during summer. A correlation between the gonadosomatic index and seawater performance, however, could not be found.

The mortality rate after saltwater exposure varied in both groups over time. In the 1-yr-old char, two of the sampled fish died during the tests in July and August. In the older fish, five died in August and three in September.

Discussion

In the present study, Arctic char of the Hornavan strain showed pronounced changes in both rheotactic behaviour and SWA throughout the year. The 2-yr-old char progressively developed a downstream behaviour during spring, followed by a marked reversal in swimming direction in August. The onset of downstream movements may be initiated by increasing water temperature. Recently, Näslund (1991) found that artificially increased temperature during March and April resulted in pronounced downstream movements in 2-yr-old Arctic char of the Hornavan strain. The seasonal pattern in rheotactic behaviour is in agreement with expectations of an anadromous migratory behaviour. In anadromous populations of Arctic char from northern Scandinavia, seaward migration occurs during May and June and the char reside for a short intensive feeding period of 1–4 mo in the estuarine or coastal waters before returning to freshwater between late July and early September (Mathisen and Berg 1968; Nordeng 1968; Jensen and Berg 1977; Berg and Berg 1989). Linnér et al. (1990) showed that younger 1-yr-old landlocked Arctic char exhibited a clear preference for moving upstream in autumn, while movements were mainly nondirectional during spring.

Arctic char show a wide variation in age at first seaward migration (Johnson 1980; Randall et al. 1987; Dempson and Kristofferson 1987). According to Nordeng (1968), anadromous char in northern Norway spend about 3–7 yr in freshwater and have a body length of 18–23 cm when they migrate to sea. The smallest char caught at sea are about 15 cm long (Nordeng 1968; Finstad et al. 1989a). In view of the wide range in age and the rather uniform size of the first-time migrants, the individual size seems to determine the onset of a seasonal migratory behaviour (Johnson 1980). The 1-yr-old char tested by Linnér et al. (1990) were raised under optimal rearing conditions and were considerably larger than fish of the same age in wild populations. However, an innate behavioural program seems only partly developed and not completely coupled to the seasonal habitat shift (Linnér et al. 1990).

SWA showed consistent seasonal variations in both age-groups. In the 2-yr-old char, these changes coincided with changes in rheotactic behaviour. During the period of pronounced downstream movements the char displayed a slight increase in regulating plasma sodium; a corresponding improvement in regulating plasma magnesium was not observed. In contrast, in late August, coinciding with a marked reversal in rheotactic behaviour, the char lost the ability to tolerate seawater, as indicated by high plasma ionic levels and a high mortality during seawater exposure. Similar variations in seawater tolerance were observed in the younger char, but a marked decrease in seawater performance occurred in this group already in July.

Older char showed a slightly better performance in the seawater challenge tests than the 1-yr-old char. These differences, however, were due to size differences between the two groups. No effect of age, except for the test in July, was found. The present results suggest that size rather than age seems to be the primary determinant of increased osmoregulatory ability. This supports the results of Conte and Wagner (1965) and McCormick and Naiman (1984) for steelhead trout (*Oncorhynchus mykiss*) and brook trout, respectively.

Similar seasonal changes in seawater tolerance have been reported by Finstad et al. (1989a) for an anadromous population of Arctic char. The authors exposed 2- to 3-yr-old char in June, September, and February to seawater at a salinity of 34‰ and a water temperature of 8°C. In June the fish were able to regulate blood plasma ionic levels within narrow limits, while in September and February, exposure to seawater resulted in marked increases in plasma ion concentrations. The present study suggests that hypoosmoregulatory capacity in the landlocked population is not developed to the same extent as in the anadromous populations, as reported by Finstad et al. (1989a). At the time of best seawater performance the plasma sodium levels in the landlocked population after 2 d in seawater (25‰) were about 10% and the magnesium levels about 40% higher compared with the control group. Similar results were found by Roberts (1971) for a landlocked population of Arctic char from the British Isles. Finstad et al. (1989b) demonstrated that a landlocked char population retained some tolerance for high salinity during summer.

In the present study the loss of seawater performance coincided with an ambient water temperature of 15–16°C. High water temperatures may have a negative effect on SWA (Hoar 1988). Johnsson and Clarke (1988) found that the optimal temperature for salinity tolerance in steelhead trout was 12–13°C and seawater survival decreased markedly when temperature exceeded 15°C. The negative effect of high temperatures could be caused by interactive effects of high metabolism and salinity as well as the temperature-dependent activity of the Na^+-K^+-ATPase in the gills (Adams et al. 1973, 1975; Jürss et al. 1984). Jensen (1981) and Berg and Berg (1989) suggested that the distribution of anadromous Arctic char in southern Norway may be limited by the prevailing high seawater temperatures. An average sea surface temperature of 14°C seems to be the upper limit for a residence of sea-run Arctic char in seawater (Jensen 1981). However, Finstad et al. (1989a) also observed a marked decrease in SWA in an anadromous population in September, although water temperature was kept constant at 8°C throughout summer and autumn. This suggests that besides temperature, other mechanisms might be involved in the loss of seawater tolerance. In the present experiment, poor seawater performance coincided with the beginning of upstream-directed movements. A lower ability to adapt to seawater during the return migration would favour a readaptation to freshwater conditions. Assuming that there is a causal relationship between these two processes, the loss in SWA could be seen as an osmoregulatory adjustment for freshwater life.

The adaptive basis of seasonal changes in seawater tolerance in a landlocked population of Arctic char is not apparent and the development of hypoosmoregulatory ability could be seen as part of a relict smoltification process. The Arctic char tested in this study have been classified as an N-type or ''normal'' char (Nyman 1972) and are considered to be closely related to the anadromous char in northern Norway (Klemetsen 1984). The apparent similarity of the migratory patterns as well as the osmoregulatory physiology suggest that, although the landlocked populations have been isolated from the sea for about 6000 yr (Ekman 1922, 1953), to a certain extent they still possess the behavioural and physiological characteristics of an anadromous sea-run char.

It has previously been suggested (McCormick and Saunders 1987) that in contrast with specialized migratory species, fish which make repeated seawater entries, such as species of the genus *Salvelinus*, seem less likely to develop preparatory physiological adaptations. McCormick et al. (1985) demonstrated that brook trout do not develop a seasonally increasing SWA and suggested that a hypoosmoregulatory capacity was developed as a result of exposure to dilute seawater. However, this seems not to be valid for all species of the genus *Salvelinus*. The results by Finstad et al. (1989a) as well as the present study clearly demonstrate that Arctic char exhibit seasonal changes in hypoosmoregulatory ability which coincide with the annual cycle of migratory behaviour.

Acknowledgements

Supported by grants from the Swedish Council of Forestry and Agricultural Research and the DFG grant (Le 196/7-1). I am indebted to Lars-Ove Eriksson and Hans Lundqvist for valuable comments on the manuscript.

References

Adams, B. L., W. S. Zaugg, and L. R. McLain. 1973. Temperature effect on parr–smolt transformation in steelhead trout (*Salmo gairdneri*) as measured by gill sodium-potassium stimulated adenosine triphosphatase. Comp. Biochem. Physiol. 44A: 1333–1339.

1975. Inhibition of salt water survival an Na-K-ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperature. Trans. Am. Fish. Soc. 104: 765–769.

Berg, O. K., and M. Berg. 1989. Sea growth and time of migration of anadromous Arctic char (*Salvelinus alpinus*) from the Vardnes River, in Northern Norway. Can. J. Fish. Aquat. Sci. 46: 955–960.

Blackburn, J., and W. C. Clarke. 1987. Revised procedure for the 24 hour seawater challenge test to measure seawater adaptability of juvenile salmonids. Can. Tech. Rep. Fish. Aquat. Sci. 1515: 35 p.

Conte, F. P., and H. H. Wagner. 1965. Development of osmotic and ionic regulation in juvenile steelhead trout, *Salmo gairdneri*. Comp. Biochem. Physiol. 14: 603–620.

Dempson, J. B., and A. H. Kristofferson. 1987. Spatial and temporal aspects of the ocean migration of anadromous Arctic char. Am. Fish. Soc. Symp. 1: 340–357.

Ekman, S. 1922. Djurvärldens utbredningshistoria på Skandinaviska halvön. Bonnier, Stockholm. 614 p. (In Swedish)

1953. Über Fischpässe in der skandinavischen Hochgebirgskette. Arch. Hydrobiol. 48: 92–96. (In German.)

Finstad, B., K. J. Nilssen, and A. M. Arnesen. 1989a. Seasonal changes in sea-water tolerance of Arctic charr (*Salvelinus alpinus*). J. Comp. Physiol. B 159: 371–378.

Finstad, B., K. J. Nilssen, and O. A. Gulseth. 1989b. Seawater tolerance in freshwater-resident Arctic charr (*Salvelinus alpinus*). Comp. Biochem. Physiol. 92A: 599–600.

Hoar, W. S. 1976. Smolt transformation: evolution, behaviour and physiology. J. Fish. Res. Board Can. 33: 1233–1252.

1988. The physiology of smolting salmonids, p. 275–343. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. XIB. Academic Press, New York, NY.

Jensen, J. W. 1981. Anadromous Arctic char, *Salvelinus alpinus*, penetrating southward on the Norwegian coast. Can. J. Fish. Aquat. Sci. 38: 247–249.

Jensen, K. W., and M. Berg. 1977. Growth, mortality and migration of the anadromous Arctic char, *Salvelinus alpinus*, L., in the Vardnes River, Troms, Northern Norway. Inst. Freshwater Res. Drottningholm Rep. 56: 70–80.

Johnson, L. 1980. The Arctic charr, *Salvelinus alpinus*, p. 15–98. *In* E. K. Balon [ed.] Charrs. Salmonid fishes of the genus *Salvelinus*. Dr. W. Junk, The Hague. The Netherlands.

Johnsson, J., and W. C. Clarke. 1988. Development of seawater adaptation in juvenile steelhead trout (*Salmo gairdneri*) and domesticated rainbow trout (*Salmo gairdneri*) — effects of size, temperature and photoperiod. Aquaculture 71: 247–263.

Jürss, K., T. Bittorf, and T. Vökler. 1984. Biochemical investigations on salinity and temperature acclimation of the rainbow trout, *Salmo gairdneri* (Richardson). Zool. Jahrb. Abt. Allg. Zool. Physiol. 88: 67–81.

Klemetsen, A. 1984. The Arctic charr speciation problem as seen from Northern Norway, p. 65–77. *In* L. J. Johnson and B. L. Bruns [ed.] Biology of Arctic charr. University of Manitoba Press, Winnipeg, Man.

Linnér, J., E. Brännas, B. S. Wiklund, and H. Lundqvist. 1990. Diel and seasonal locomotor activity patterns in Arctic charr (*Salvelinus alpinus* L.). J. Fish Biol. 37: 675–685.

Lundqvist, H., and L.-O. Eriksson. 1985. Annual rhythms of swimming behaviour and seawater adaptation in young Baltic salmon, *Salmo salar*, associated with smolting. Environ. Biol. Fishes 14: 259–267.

Mathisen, O. A., and M. Berg. 1968. Growth rates of the char *Salvelinus alpinus* (L.) in the Vardnes River, Troms, Northern Norway. Inst. Freshwater Res. Drottningholm Rep. 48: 177–186.

McCormick, S. D., and R. J. Naiman. 1984. Osmoregulation in the brook trout, *Salvelinus fontinalis* — II. Effects of size, age and photoperiod on seawater survival and ionic regulation. Comp. Biochem. Physiol. 79A: 17–28.

McCormick, S. D., R. J. Naiman, and E. T. Montgomery. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 42: 529–538.

McCormick, S. D., and R. L. Saunders. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism, Am. Fish. Soc. Symp. 1: 211–229.

Näslund, I. 1991. Effects of temperature, season and feeding situation on the rheotactic behaviour of two stocks of landlocked Arctic charr. Nord. J. Freshwater Res. 66: 108–114.

Nordeng, H. 1968. Arctic charr (*Salvelinus alpinus* L.), p. 1237–1248. *In* K. W. Jensen [ed.] Sportfiskerens Leksikon. Gyldendal Norsk Forlag. (In Norwegian)

Nyman, L. 1972. A new approach to the taxonomy of the "*Salvelinus alpinus* species complex." Inst. Freshwater Res. Drottningholm Rep. 52: 103–131.

Randall, R. G., M. C. Healey, and J. B. Dempson. 1987. Variability in length of freshwater residence of salmon, trout and char. Am. Fish. Soc. Symp. 1: 27–41.

Roberts, R. A. 1971. Preliminary observations on the ionic regulation of the Arctic char *Salvelinus alpinus*. J. Exp. Biol. 55: 213–222.

Rounsefell, G. A. 1958. Anadromy in North American Salmonidae. U.S. Fish Wildl. Serv. Fish. Bull. 58(131): 171–185.

Wilkinson, L. 1988. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.

Swimming Behavior of Coho Salmon, *Oncorhynchus kisutch*, in the Open Sea as Determined by Ultrasonic Telemetry[1]

Miki Ogura and Yukimasa Ishida

National Research Institute of Far Seas Fisheries, Japan Fisheries Agency, 5-7-1, Orido, Shimizu, Japan 424

Ogura, M., and Y. Ishida. 1992. Swimming behavior of coho salmon, *Oncorhynchus kisutch*, in the open sea as determined by ultrasonic telemetry. Can. J. Fish. Aquat. Sci. 49: 453–457.

Four coho salmon, *Oncorhynchus kisutch*, with depth-sensing ultrasonic transmitters were tracked in the central North Pacific Ocean during June and early July 1989. The average swimming depths of the fish ranged from 7.1 to 13.4 m, and they spent 72.3–92.8% of the time in the upper 15 m of the water column; maximum depths were 53–74 m. Average ground speeds ranged from 0.29 to 0.40 $m \cdot s^{-1}$. Although swimming depths during the day were deeper than at night, one coho salmon tracked for 5 d showed no regular daily patterns of horizontal or vertical movements.

On a suivi les déplacements de quatre saumons cohos, *Oncorhynchus kisutch*, munis de transmetteurs ultrasoniques de la profondeur dans le centre-nord du Pacifique en juin et au début de juillet 1989. La profondeur moyenne fréquentée par les saumons variait de 7,1 à 13,4 m et ils ont passé de 72,3 à 92,8% de leur temps dans les 15 m supérieurs de la colonne d'eau; la profondeur maximale frquentée allait de 53 à 74 m. La vitesse moyenne de déplacement au sol allait de 0,29 à 0,40 $m \cdot s^{-1}$. Quoique la profondeur fréquentée pendant le jour était plus élevée que pendant la nuit, un coho suivi pendant 5 jours n'a pas présenté de régime quotidien régulier de déplacements horizontaux ou verticaux.

Received April 25, 1991
Accepted October 10, 1991
(JB014)

Reçu le 25 avril 1991.
Accepté le 10 octobre 1991

Coho salmon, *Oncorhynchus kisutch*, are the fourth most abundant species of Pacific salmon. The center of abundance in Asia is the Kamchatka Peninsula, and in North America they are found mainly from Oregon to southeast Alaska. Most coho salmon spend 1 or 2 yr in freshwater before migrating to sea. They, like pink salmon, *Oncorhynchus gorbuscha*, return to spawn after spending one winter in the ocean (Godfrey et al. 1975). Therefore, coho salmon in their second year of ocean life are maturing fish.

While the behavior and orientation mechanisms of salmon in coastal waters are partially understood, in the open sea, no telemetry study for salmonids has been conducted and even less direct information is available on the behavior of salmon. The purpose of this study was to describe the vertical and horizontal movements of maturing coho salmon in the open sea by ultrasonic telemetry.

Materials and Methods

The tracking was conducted by the Japanese salmon research vessel *Shin-riasu maru* (471 gross tonnes, 48 m in length) between June 12 and July 5, 1989, in the area bounded by 43–46°N latitude and 175–177°W longitude in the North Pacific. Four coho salmon (511–571 mm fork length) caught by longline were used and were designated as Nos. 8902, 8903, 8904, and 8905 (Table 1). Telemetry data for three coho salmon (Nos. 8902, 8903, and 8904) ended within 2 d when the fish were lost because of foul weather. Data for the remaining coho salmon (No. 8905) ended when the fish was lost after 5 d because of foul weather and decreasing transmitter strength due to the battery life limit. Because of the long track record from this coho salmon, more detailed information is presented for it than for the other three fish.

TABLE 1. Fork length and age of tracked coho salmon, and duration, direction, and distance of tracking.

Salmon No.	Fork length (mm)	Age[a]	Duration (h:min)	Net direction[b]	Net distance[c] (km)	Gross distance[d] (km)
8902	511	1.1	20:49	90°	16.9	30.1
8903	571	1.1	36:55	30°	36.4	51.4
8904	537	1.1	24:22	90°	9.6	24.4
8905	560	2.1	133:30	185°	88.0	177.2

[a] The number preceding the point is the number of winter annuli spent in freshwater and the number following the point is the number of winter annuli spent in the ocean (Koo 1962).

[b] The direction from the point of release to the point where the fish was lost, in degrees relative to geographic north.

[c] The shortest distance from the point of release to the point where the fish was lost.

[d] The total distance tracked.

The transmitters (Vemco Ltd., Dartmouth, Nova Scotia, Canada) were cylindrical (length 65 mm, diameter 15 mm) and weighed 23 g (underwater weight 11 g). They operated on a carrier frequency of 50 kHz for 5 d and the pulse intervals were proportional to water depth. The transmitter was attached externally, immediately anterior to the dorsal fin.

The tracking was conducted with a receiver and three directional hydrophones (Vemco, Ltd.) at the bottom of a pole, which was mounted on the starboard side of the research vessel

---

[1] An earlier version of this paper was submitted to the Annual Meeting of the International North Pacific Fishery Commission, Seattle, WA, October 1989.

TABLE 2. Vertical movements of coho salmon tracked using ultrasonic transmitters.

Salmon No.	Average swimming depth (m)			Maximum swimming depth (m)	Speed of vertical movement ($\mathrm{m \cdot min^{-1}}$)			
					Average[a]		Initial dive	
	Overall	Day	Night		Dive	Ascent	Dive	Ascent
8902	8.3	10.6	5.4	60	3.4	4.6	9.3	4.7
8903	13.4	13.9	12.4	74	4.9	4.7	7.3	11.4
8904	7.1	7.6	6.1	53	5.7	5.0	No dive	
8905	8.1	9.5	5.2	58	3.8	4.2	No dive	
Mean	9.2	10.4	7.3		4.5	4.6		

[a]Calculated from data excluding the initial dive.

and submerged 3 m under the surface with 10, 45, and 80° of downward angle, respectively. Hydrophones were switched periodically in accordance with the swimming depth of the fish. The direction of the fish was confirmed by changing the direction of the hydrophone by turning the pole. The output of a digital signal on time and swimming depth from the receiver was recorded on a personal computer diskette at 5-s intervals. Average swimming depths during every 1 min were used in the following analysis. The vessel's locations were recorded by Navy Navigation Satellite System (NNSS) as often as satellite information was available (average interval 44 min). Water temperatures were measured to a depth of 250 m before and after tracking the fish. While tracking a fish, water temperature profiles were recorded using expendable bathythermographs at least every 12 h.

The position of the vessel tracking the fish was regarded as the horizontal location of the fish. Since the range of transmitters used in this study was 500–600 m (based on the field experiment using a transmitter suspended 20 m from the surface by a radar reflecting buoy) and since there were some navigational errors, recording the vessel's position at intervals of less than 30 min was meaningless (Ishida et al. 1988; Hawkins and Urquhart 1983). Therefore the vessel's recorded position was used at intervals of more than 30 min, as in Ishida et al. (1988), and the maximum interval was 192 min.

The directional index is calculated by dividing the net distance (shortest distance from the point of release to the point where the fish was lost) by the gross distance (total distance tracked).

Results

Vertical Movements

The four coho salmon confined their movements to the upper 53–74 m of the water column and they were generally near the surface with average depths from 7.1 to 13.4 m (Table 2). Maximum depths were 53–74 m. For each fish, average swimming depths in daytime tended to be deeper than in nighttime (t-test, $P < 0.05$; using the logarithmically transformed data $X' = \log (X + 1)$). Two coho salmon (Nos. 8902 and 8903) made steep dives to 55 and 45 m immediately after release, respectively. Vertical speeds during these initial dives (maximum $11.4\ \mathrm{m \cdot min^{-1}}$) were faster than average vertical speeds ($3.4–5.7\ \mathrm{m \cdot min^{-1}}$) calculated without data during the initial dive. The other two coho salmon did not show such steep dives after release. Although thermoclines were not stable at these locations, three coho salmon spent from 73.1 to 87.6% of the time in the upper 10 m of the water column (Fig. 1). Coho salmon No. 8903 spent 41.2% of the time in the upper 10 m but spent a total of 72.3% of the time in the upper 15 m.

Coho salmon No. 8905 repeatedly dived and returned to the surface over the first 7 h after release (Fig. 2). Thereafter, it generally remained near the surface except for occasional brief dives to 30–50 m or for longer periods at 30–40 m. From nighttime of the third day to the fourth day and nighttime of the fifth day, it rarely dived, and swimming depths were much shallower than overall averages and fewer vertical movements were observed (Table 3).

Horizontal Movements

Coho salmon No. 8902 and 8904 generally moved eastward. Coho salmon No. 8903 first moved northeast and then moved northward. The track of No. 8905 (Fig. 3) showed a movement south from the release point on a semicircular path during the first 3 d and thereafter a southward movement.

The directional speeds, calculated from the net distances, ranged from 9.5 to $23.7\ \mathrm{km \cdot d^{-1}}$ (Table 4). Ground speeds were calculated by dividing the gross distances by the durations. Average ground speeds for each fish in daytime and nighttime were similar at about $0.36\ \mathrm{m \cdot s^{-1}}$. All four fish showed higher directional indices at night than during the day.

The ground speed and directional index of No. 8905 varied for each day and night, but did not show daily patterns (Table 3). Ground speeds during daytime of the first day, daytime and nighttime of the second day, and daytime of the fifth day of tracking were greater than the overall average. The directional index of daytime on the first day was lowest and that of daytime on the third day was highest. Thereafter, it was less variable.

Discussion

The coho salmon in this study inhabited near-surface waters (above 74 m at the deepest). Although average swimming depths in the daytime were deeper than at night, no regular daily changes in swimming depths were observed. Based on catch data of longlines and gill nets, Godfrey et al. (1975) reported that Pacific salmon extend their vertical distribution downward in daytime. However, many salmon were caught in the surface layer even in daytime.

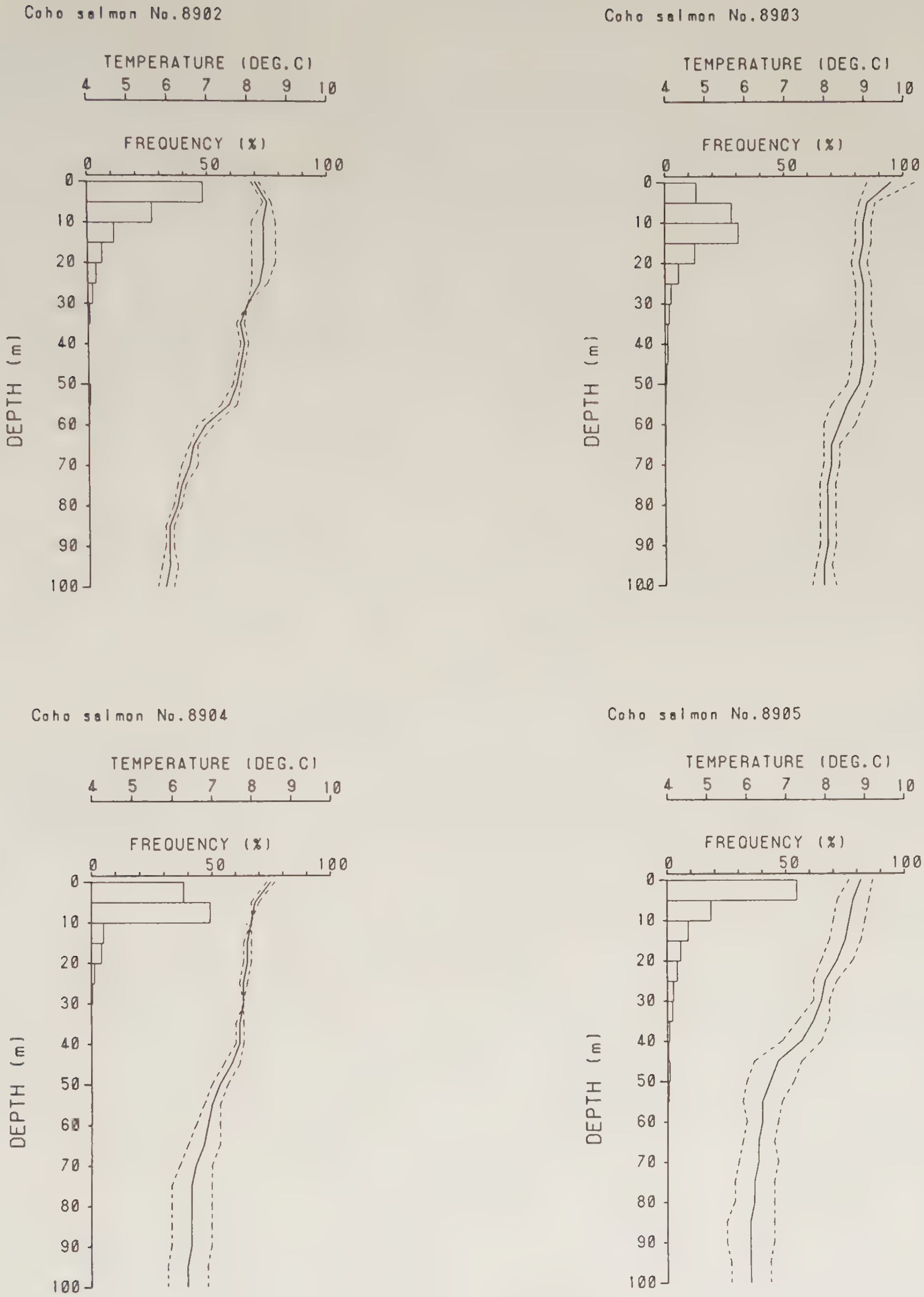


FIG. 1. Depth distributions (bars), expressed as a percentage of records averaged during 1 min of four coho salmon (Nos. 8902, 8903, 8904, and 8905) tracked in relation to the vertical profiles of temperature. Solid and broken lines indicate average and ± 1 SD, respectively.

There is no consistent diel pattern of vertical distribution for all species of Pacific salmon or individuals within a species (Ichihara et al. 1975; Quinn et al. 1989; Ruggerone et al. 1990). Since feeding and migration are major motivations of vertical movement, the variation of daily changes may occur due to stage of maturity, food and physical environments, and the distance from natal rivers.

On the basis of predominantly daytime movements of steelhead trout, *Oncorhynchus mykiss*, in coastal waters, Ruggerone et al. (1990) suggested that the sun and polarized light might be involved in orientation. However, in the present study the directional indices showed that coho salmon maintained relatively constant courses during both the day and night, suggesting that coho salmon use directional cues which function at both times of day. Similar results were reported for swordfish, *Xiphias gladius*; they maintained constant compass courses for substantial periods (Carey and Robison 1981).

The directional speeds in this study (9.5–23.7 $\mathrm{km \cdot d^{-1}}$) were slower than those (24–30 $\mathrm{km \cdot d^{-1}}$) during homeward migration estimated from tag recovery data (Godfrey et al. 1975). Ground speeds (0.29–0.40 $\mathrm{m \cdot s^{-1}}$) estimated for coho salmon in the present study were also slower than that (1.6 $\mathrm{m \cdot s^{-1}}$) of one

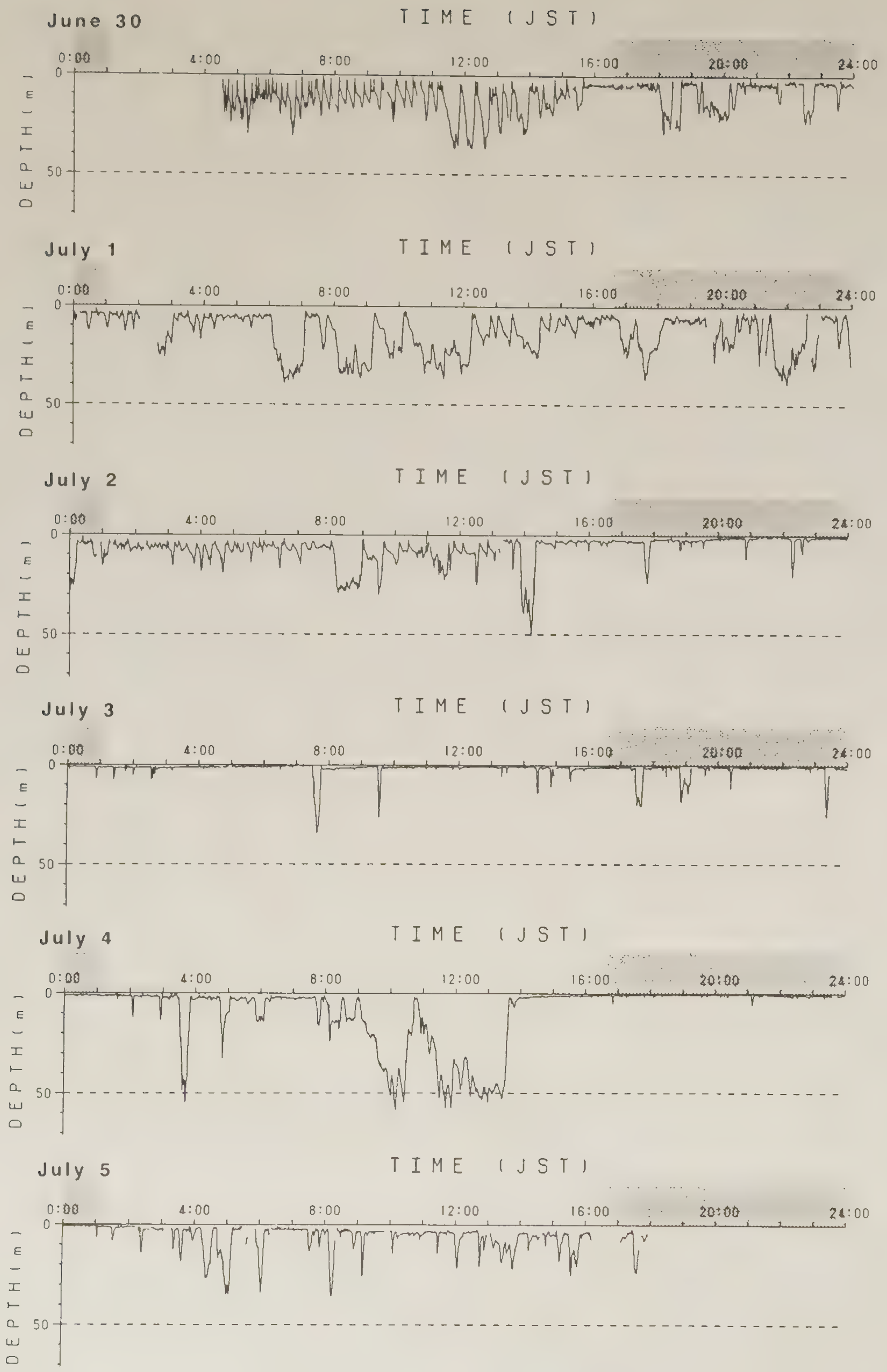


FIG. 2. Vertical movement of tracked coho salmon No. 8905. Shaded time zones indicate nighttime. JST Japan standard time.

chum salmon during the last part of the homeward migration in the open sea (Ichihara et al. 1975). An acceleration in rate of travel as the maturing sockeye salmon, *Oncorhynchus nerka*, approach shore was reported in tagging data analysis (French et al. 1976). Swimming speeds estimated by ultrasonic telemetry in coastal waters varied from 0.28 to 1.51 $m \cdot s^{-1}$ (Ichihara et al. 1982; Soeda et al. 1987; Ishida et al. 1988; Quinn et al. 1989; Ruggerone et al. 1990). The relatively slow directional speeds observed in this study suggest that coho salmon migrate more slowly in the open sea than they do in coastal waters, perhaps because they have not yet begun their spawning migration in June and early July.

TABLE 3. Swimming depth, ground speed and directional index of coho salmon No. 8905 during day and night for each date.

Date	Swimming depth		Ground speed (m·s^{-1})[a]		Directional index[b]	
	Day	Night	Day	Night	Day	Night
June 30	12.5	7.8	0.43	0.23	0.42	0.69
July 1	14.4	13.9	0.46	0.43	0.69	0.83
July 2	8.9	2.1	0.37	0.34	0.96	0.56
July 3	1.5	1.9	0.26	0.31	0.72	0.69
July 4	13.8	0.5	0.46	0.31	0.78	0.69
July 5	6.4	—	0.36	—	0.61	—
Overall average	8.1		0.37		0.71	

[a] Calculated by dividing gross distance by duration.
[b] Calculated by dividing net distance by gross distance.

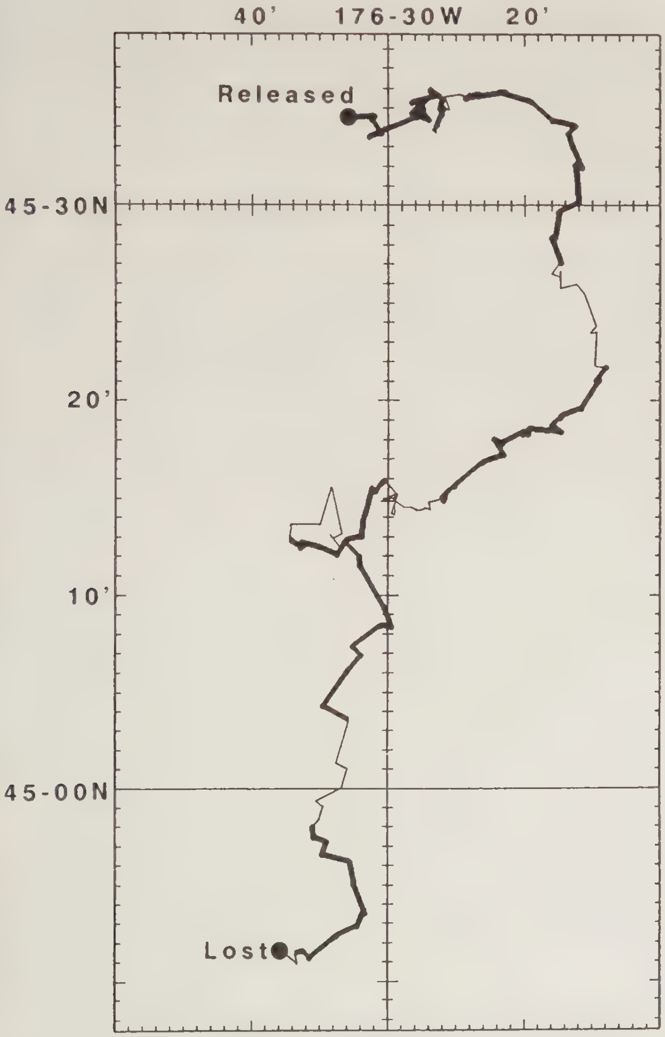


FIG. 3. Track of the research vessel *Shin-riasu maru* while following coho salmon No. 8905. Thick and thin lines indicate tracks during day and night, respectively.

TABLE 4. Horizontal movements of coho salmon tracked using ultrasonic transmitters.

Salmon No.	Directional speed (km·d^{-1})[a]	Average ground speed (m·s^{-1})[b]			Average directional index[c]	
		Overall	Day	Night	Day	Night
8902	19.5	0.39	0.38	0.41	0.56	0.72
8903	23.7	0.40	0.39	0.42	0.85	0.96
8904	9.5	0.29	0.29	0.28	0.33	0.94
8905	15.8	0.37	0.39	0.33	0.70	0.72
Mean	17.1	0.36	0.36	0.36	0.61	0.84

[a] Calculated by dividing net distance by duration.
[b] Calculated by dividing gross distance by duration.
[c] Calculated by dividing net distance by gross distance.

Acknowledgments

We heartily thank Captain Yoshinobu Muraki of the research vessel *Shin-riasu maru* and his crew who worked day and night for the tracking. We wish to thank Dr. Kazumoto Yoshida of the Nansei National Fisheries Research Institute and Mr. Takashi Koido of Nagasaki University for their valuable advice on the telemetry system. We are also grateful to Ms. Nancy Davis of the Fisheries Research Institute, University of Washington, for reviewing an earlier draft of this paper and to Dr. Thomas Quinn of the University of Washington for critically reading the manuscript.

References

CAREY, F. G., AND B. H. ROBISON. 1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry, U.S. Fish. Bull. 79: 277–292.

FRENCH, R., H. BILTON, M. OSAKO, AND A. HARTT. 1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 34: 113 p.

GODFREY, H., K. A. HENRY, AND S. MACHIDORI. 1975. Distribution and abundance of coho salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 31: 80 p.

HAWKINS, A. D., AND G. G. URQUHART. 1983. Tracking fish at sea, p. 103–166. *In* A. G. Macdonald and I. G. Priede [ed.] Experimental biology at sea. Academic Press, London.

ICHIHARA, T., A. NAKAMURA, AND S. TANAKA. 1982. Analysis of behavior of adult chum salmon by biotelemetry, p. 79–87. *In* Final report of special salmon study [SAKE BETSUWAKU SOKATSU HOUKOKU]. Japan Fish. Agency, Tokyo, Japan, March 1982. (In Japanese)

ICHIHARA, T., T. YONEMORI, AND H. ASAI. 1975. Swimming behavior of a chum salmon, *Oncorhynchus keta*, on the southern migration off Etorofu Island, the southern Kurils Islands. Bull. Far Seas Fish. Res. Lab. 13: 63–77. (In Japanese with English summary)

ISHIDA, K., S. NAGAHORA, Y. INOUE, AND T. WATANABE. 1988. Behavior of adult chum salmon *Oncorhynchus keta* homing to the coast of Sanriku. Nippon Suisan Gakkaishi 54: 1279–1287. (In Japanese with English summary)

KOO, T. S. Y. 1962. Age designation in salmon, p. 37–48. *In* T. S. Y. Koo [ed.] Studies of Alaska red salmon. University of Washington Press, Seattle, WA.

QUINN, T. P., B. A. TERHART, AND C. GROOT. 1989. Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. Anim. Behav. 37: 587–599.

RUGGERONE, G. T., T. P. QUINN, I. A. MCGREGOR, AND T. D. WILKINSON. 1990. Horizontal and vertical movements of adult steelhead trout, *Oncorhynchus mykiss*, in the Dean and Fisher channels, British Columbia. Can. J. Fish. Aquat. Sci. 47: 1963–1969.

SOEDA, H., K. YOZA, T. SHIMAMURA, AND E. HASEGAWA. 1987. On the swimming behavior of chum salmon in early migratory season off the coast of Hokkaido, Okhotsk Sea. Nippon Suisan Gakkaishi 53: 1827–1833.

Stunting of Wild Coho Salmon (*Oncorhynchus kisutch*) in Seawater: Patterns of Plasma Thyroid Hormones, Cortisol, and Growth Hormone

Vladimir S. Varnavsky

Laboratory of Salmon Ecophysiology, Institute of Marine Biology, 68300 Peteropavlovsk-Kamchatsky, USSR

and Tatsuya Sakamoto[1] and Tetsuya Hirano

Ocean Research Institute, University of Tokyo, Nakano, Tokyo 164, Japan

Varnavsky, V. S., T. Sakamoto, and T. Hirano. 1992. Stunting of wild coho salmon (*Oncorhynchus kisutch*) in seawater: patterns of plasma thyroid hormones, cortisol, and growth hormone. Can. J. Fish. Aquat. Sci. 49: 458–461.

Under natural conditions, some coho salmon presmolts (*Oncorhynchus kisutch*) in Kamchatka have been observed to migrate prematurely to the sea and fail to grow in brackish water for prolonged periods (natural stunts). Plasma levels of growth hormone, cortisol, thyroxine, and triiodothyronine were measured in coho salmon parr captured in the river (freshwater), smolts migrating downstream captured at the river mouth (brackish water), smolts in the sea (seawater), and natural stunts in the inlet (brackish water). The physiological conditions of natural stunts seem analogous to those of hatchery-derived stunts observed in hatchery-reared juveniles in sea pens, with normal plasma sodium concentration, low levels of thyroid hormones and cortisol, and high growth hormone levels.

À l'état naturel, certains pré-smolts du saumon coho (*Oncorhynchus kisutch*) de la Kamchatka migrent prématurément vers la mer et voient leur croissance en eaux saumâtres s'arrêter pendant de longues périodes. Les teneurs plasmatiques d'hormone de croissance, de cortisol, de thyroxine et de triiodothyronine ont été déterminées chez des tacons de coho capturés dans le cours d'eau (eau douce), des smolts en migration vers l'aval capturés à l'embouchure (eau saumâtre), des smolts en mer (eau de mer) et des individus à croissance arrêtée capturés dans l'inlet (eau saumâtre). Les conditions physiologiques des individus à croissance arrêtée semblent analogues à celles des poissons d'élevage à croissance arrêtée que l'on observe à l'état de juvéniles dans les cages en mer; les concentrations plasmatiques de sodium sont normales, celles des hormones de la thyroïdes et du cortisol sont faibles et celles de l'hormone de croissance sont élevées.

Received June 14, 1991
Accepted October 10, 1991
(JB082)

Reçu le 14 juin 1991
Accepté le 10 octobre 1991

Coho salmon (*Oncorhynchus kisutch*) juveniles must complete parr–smolt transformation prior to seawater entry in order to thrive and grow in seawater (Folmar and Dickhoff 1980). In coho salmon rearing on the west coast of North America, premature transfer of young fish to sea pens, before full transformation into smolts, often results in high initial mortality and/or considerable stunting among the survivors (Bern 1978). In addition, later reversion of smolts (''parr-revertants'') held in seawater also occurs (Mahnken et al. 1970; Folmar et al. 1982; Hoar 1988). Physiological and morphological characteristics of the ''stunt'' and ''parr-revertant'' have been examined rather extensively in the past two decades (see Hoar 1988).

Although there has been no report of stunted coho salmon parr in seawater prior to the advent of net-pen culture, Folmar et al. (1982) considered that they could occur naturally and not solely as the result of intensive culture. In wild populations of the Paratunka River, Kamchatka, both presmolts and smolts usually start downstream migration; most of the former complete smoltification quickly during downstream migration or in the estuary. They stay in the estuary for a few days and then migrate to the ocean. Some fish, presumably presmolts which have not completed their smoltification, stay stunted (natural stunts) in brackish water for about 1 mo (Varnavsky 1989). It is highly proabable that such intrapopulational heterogeneity in smolt quality of wild coho salmon is reflected in hormonal status and osmoregulatory ability, as occurs in abnormal smoltification of hatchery-reared coho salmon: the stunts have been diagnosed as pan-hypoendocrine with a few notable exceptions, one of which is the consistently high growth hormone (GH) cell activity in the pituitary as well as high plasma GH levels (Clarke and Nagahama 1977; Bern 1978; Nishioka et al. 1982; Bolton et al. 1987; Young et al. 1989b). Stunting has been repeatedly linked to osmoregulatory dysfunction, although plasma ion profiles generally appear to be normal (Clarke and Nagahama 1977; Marini and Kerstetter 1982). Similar stunting problems have been reported in Atlantic salmon (*Salmo salar*) in Iceland (Björnsson et al. 1988). In the present study, changes in the plasma levels of GH, thyroid hormones, and cortisol were examined in (1) wild coho salmon parr captured in the river, (2) smolts just after downstream migration captured at the river mouth, (3) natural stunts in brackish water, and (4) smolts in the sea.

---

[1] Author to whom correspondence should be addressed: Ocean Research Institute, University of Tokyo, 1-15-1, Minamidai, Nakano-ku Tokyo 164, Japan.

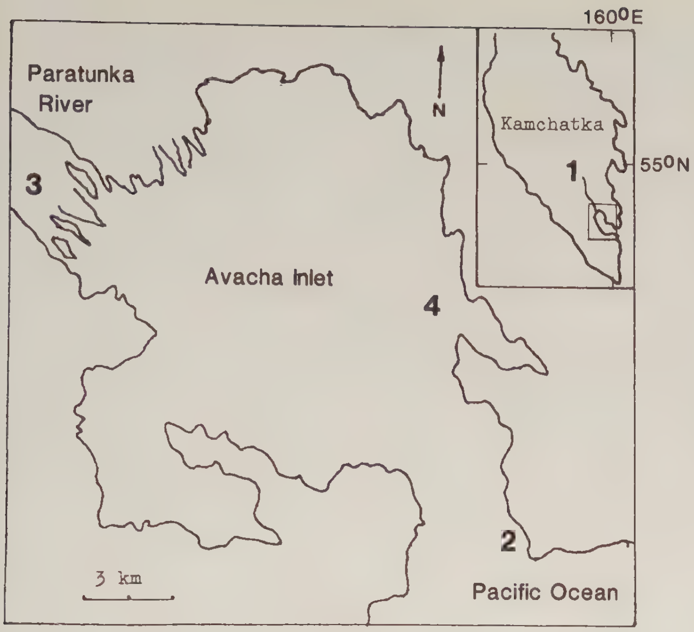


FIG. 1. Location of the sampling stations. The salinities measured by refractometer were (2) 28–30‰, (3) 0.5–5‰, and (4) 24–28‰.

Materials and Methods

Yearling coho salmon were caught in the Paratunka River, in the river mouth, and in the Avacha Inlet, Kamchatka (Fig. 1). Salinity was measured by a refractometer. The fish were classified into four groups as judged by morphological characteristics (cf. Gorbman et al. 1982) as parr, ''migrating'' smolts, seawater smolts, and natural stunts in the estuary. A beach-seine was used to catch parr in May in the upper Paratunka River (station 1, freshwater) and seawater smolts in July in Avacha Inlet (station 2, salinity 28–30‰). ''Migrating'' smolts were collected in June by a trap at the river mouth (station 3, salinity 0.5–5‰). Natural stunts were captured at the end of August in the zone of variable salinity of Avacha Inlet (station 4, salinity 24–28‰) by a beach-seine by selecting small yearlings with morphological characteristics similar to seawater parr described by Gorbman et al. (1982). Migrating fish were collected at station 3 every week from April to July; no fish were caught after the beginning of August. Thus, the fish caught at station 4 at the end of August must have resided in brackish water for at least 1 mo.

The fish were transported in tanks containing the water from the capture area to the laboratory located on the eastern coast of the Inlet. One to two hours after capture, they were anesthetized with MS222, the tail was severed, and blood was collected into microhematocrit tubes treated with ammonium-heparin. After centrifugation at 3000 rpm for 3 min, plasma was taken and stored in liquid nitrogen.

Plasma sodium concentration was measured using an atomic absorption spectrophotometer (Hitachi 180-150). Plasma levels of GH, cortisol, triiodothyronine (T_3), and thyroxine (T_4) were measured by radioimmunoassays following Bolton et al. (1986), Takahashi et al. (1985), and Tagawa and Hirano (1987, 1990), respectively. Condition factor was calculated by the formula ($W/L^3 \times 100$ where W is weight in grams and L is fork length in centimetres. Data are presented as means ± standard errors. Statistical significance was examined by one-way analysis of variance (ANOVA) and the Kruskal–Wallis test for multiple groups.

Results and Discussion

Migrating smolts caught at the river mouth and natural stunts in the Inlet were significantly thinner than parrs and smolts in seawater as judged by condition factor (Table 1), although they were not so ''pinheaded'' as described by Gorbman et al. (1982) for hatchery stunted coho salmon. The smolts in the river mouth and in seawater were silvery with dark fin margins; no parr marks were observed. Stunts differed from both groups of smolts by the appearance of faint parr marks. Smolts were metallic blue on their dorsal surface whereas stunts were brown.

The parr in freshwater had lower plasma sodium levels than the smolts at the river mouth or in seawater and natural stunts. There were no significant differences in plasma sodium concentrations between smolts and stunts (Table 2). Thus the natural stunts seem to possess normal hypoosmoregulatory capacity. These results are consistent with observations on hatchery-reared stunts of coho salmon (Clarke and Nagahama 1977). According to Marini and Kerstetter (1982), however, intracellular potassium levels in liver were significantly higher in coho salmon sunts in seawater than in smolts in seawater or in freshwater. Hypoosmoregulatory ability seems to be severely impaired in stunts of Atlantic salmon (Björnsson et al. 1988). Intracellular ion levels were not measured in the present study.

Plasma GH levels were significantly higher in migrating smolts caught at the river mouth in June than in parr caught earlier in the river whereas the levels in smolts caught in seawater in July were as low as in the parr. Similarly, low levels of GH were observed in mature fish caught at station 2 in September, weighing about 3 kg, returning from the ocean (7.3 ± 1.3 ng/mL, n = 14). The elevation of GH level in migrating smolts caught at the river mouth presumably reflected developmental and osmoregulatory changes during smoltification and downstream migration. Elevated plasma GH levels have been reported during smoltification in hatchery-reared coho salmon (Sweeting et al. 1985; Young et al. 1989a) and could be considered as ''preadaptive'' for entry into seawater (Young et al. 1989a). Sweeting et al. (1985) and Sakamoto et al. (1991) observed an increase in plasma GH levels after transfer of coho salmon smolts from freshwater to seawater whereas Young et al. (1989a) reported no such increase. A complete assessment of GH dynamics requires evaluation of the plasma metabolic clearance rate and secretion rate of GH from the pituitary, in addition to plasma hormone concentrations. The metabolic clearance rate of GH is higher in coho salmon smolts in seawater than in the fish in freshwater (Sakamoto et al. 1991). Coho salmon smolts of this population in Kamchatka showed maximal growth rate soon after entry into seawater (Varnavsky 1989). Therefore, the plasma GH concentrations in seawater smolts that are lower than in ''migrating'' smolts could reflect a higher rate of clearance of the hormone, which is involved in growth promotion in the marine environment. A reduction in plasma GH levels during prolonged periods (2–3 wk) of acclimation to seawater has also been reported for coho salmon smolts (Young et al. 1989a; Sakamoto et al. 1991).

Stunts show numerous signs of a pan-hypoendocrine state with the exception of highly activated GH cells in the pituitary (Clarke and Nagahama 1977; Nishioka et al. 1982) and possible hyperactivity of Stannius corpuscles (see Aida et al.

TABLE 1. Profiles of wild coho salmon from the Paratunka River and Avacha Inlet. Data are presented as means ± SEM. Values sharing a common superscript are not significantly different by one-way ANOVA and Kruskal–Wallis test at $P < 0.05$.

Group	Date (1990)	Station	Salinity (‰)	n	Weight (g)	Length (cm)	Condition factor $(W/L^3) \times 100$
Parr	22 May	Upper Paratunka River (station 1)	0	31	5.6 ± 0.3^a	7.6 ± 0.3^a	1.13 ± 0.03^a
"Migrating" smolts	18 June	Mouth of Paratunka River (station 3)	0.5–5	30	13.3 ± 0.2^b	11.0 ± 0.2^b	0.96 ± 0.02^b
Seawater smolts	14 July	Avacha Inlet (station 2)	28–30	16	27.5 ± 3.1^c	13.2 ± 0.5^c	1.11 ± 0.02^a
Stunts	27 August	Avacha Inlet (station 4)	24–28	18	13.3 ± 0.6^b	11.0 ± 0.2^b	0.99 ± 0.02^b

TABLE 2. Plasma sodium concentration (mmol/L) and hormone levels (ng/mL) of coho salmon at different life stages. GH, growth hormone; T_4, thyroxine; T_3, triiodothyronine. Values in parentheses are numbers of samples. Data are presented as means ± SEM. Values sharing a common superscript are not significantly different by one-way ANOVA and Kruskal–Wallis test at $P < 0.05$.

Group	Sodium	GH	T_4	T_3	Cortisol
Parr	138 ± 15.2^a (4)	13.7 ± 2.3^a (6)	$0.7 \pm 0.4^{a,b}$ (3)	0.2 ± 0.1^a (2)	5.8 ± 0.8^a (6)
"Migrating" smolts	167 ± 7.2^b (8)	55.0 ± 8.5^b (7)	$3.9 \pm 1.4^{a,c}$ (8)	1.5 ± 0.5^b (8)	64.7 ± 21.5^b (8)
Seawater smolts	169 ± 9.5^b (15)	11.7 ± 1.8^a (12)	2.3 ± 0.6^c (16)	3.9 ± 0.6^c (16)	47.9 ± 9.7^b (16)
Stunts	168 ± 5.1^b (17)	41.5 ± 9.0^b (8)	0.3 ± 0.1^b (17)	$0.3 \pm 0.1^{a,b}$ (17)	42.0 ± 13.6^b (17)

1980). Plasma GH levels in stunts were significantly higher than in seawater smolts, being as high as in "migrating" smolts. This is in accord with previous reports on high plasma GH levels in hatchery-derived stunts in coho and Atlantic salmon produced by premature transfer to seawater (Bolton et al. 1987; Björnsson et al. 1988; Young et al. 1989b). Reduced GH-binding sites have been reported in liver, gill, and kidney of coho salmon stunts as compared with those of smolts (Fryer and Bern 1979; Gray et al. 1990). The decreased binding of GH to receptor sites may be the main cause of growth cessation in stunts, and this may have contributed to or resulted from the elevated GH levels.

Higher plasma levels of both T_4 and T_3 in smolts in seawater and at the river mouth than in freshwater parr (Table 2) are in good agreement with previous work, supporting the probable role of thyroid hormones in smoltification of salmonids (Hoar 1988; Young et al. 1989a). Specker and Kobuke (1987) found that transfer of fully smolted coho salmon to seawater resulted in enhanced thyroid activity, although there is no explanation for the higher plasma level of T_3 in smolts in seawater than at the river mouth. In contrast, T_4 levels in stunts were eightfold lower than in seawater smolts in the present study. A similar tendency was observed in T_3 levels. Decreased thyroid activity has also been observed in hatchery-derived stunts of coho and Atlantic salmon (see Hoar 1988; Björnsson et al. 1988; Young et al. 1989b).

The transition from the parr to the smolt stage was also accompanied by an elevation of plasma cortisol concentration (Table 2). Although we cannot exclude the possible stress response after capture on plasma levels of the hormones (Leatherland 1985; Donaldson 1981; Pickering et al. 1991), the cortisol levels observed in this study were within the normal (unstressed) range. The higher cortisol level in smolts than in parr is in agreement with the well-defined increase in plasma cortisol during smoltification (see Hoar 1988; Young et al. 1989a), and elevation of plasma cortisol has been repeatedly observed after seawater entry of coho salmon smolts (Redding et al. 1984; Young 1985; Young et al. 1989a, 1989b). Plasma cortisol levels in stunts appeared slightly lower than in smolts, although the differences were not statistically significant (Table 2). As part of their pan-hypoendocrine state, hatchery-derived coho salmon stunts exhibit cytological evidence of interrenal hypoactivity (Nishioka et al. 1982), although the reduction in plasma cortisol levels is not always consistent (Young et al. 1989b).

The physiological conditions in "natural" coho salmon stunts seem analogous to those of stunts arising from premature transfer of hatchery-reared juveniles to seawater. It is likely that some premature juveniles of wild coho salmon may enter seawater together with fully smolted fish, thus resulting in "natural" stunts. Hatchery-derived stunts transferred back to freshwater resume normal growth (Clarke and Nagahama 1977; Young et al. 1989b). Under natural conditions, some masu salmon (*Oncorhynchus masou*) have been observed to return from seawater to freshwater (Kubo 1974). We have no explanation as to why "natural" stunts of coho salmon remain in their hyperosmotic environment, instead of returning to freshwater.

Acknowledgments

We are grateful to Professor Howard A. Bern, University of California, Berkeley, CA, and Dr. W. Craig Clarke, Pacific Biological Station, Fisheries and Oceans, Nanaimo, B.C., for reading of the manuscript. Financial assistance for this study was provided in part by grants-in-aid for scientific research from the Ministry of Education, Science and Culture, and also from the Fisheries Agency, Japan.

References

AIDA, K., R. S. NISHIOKA, AND H. A. BERN. 1980. Changes in the corpuscles of Stannius of coho salmon (*Oncorhynchus kisutch*) during smoltification and seawater adaptation. Gen. Comp. Endocrinol. 41: 296–304.

BERN, H. A. 1978. Endocrinological studies on normal and abnormal salmon smoltification, p. 97–100. *In* P. J. Gaillard and H. H. Boer [ed.] Comparative endocrinology. Elsevier, Amsterdam, The Netherlands.

Björnsson, B. Th., T. Ogasawara, T. Hirano, J. P. Bolton, and H. A. Bern. 1988. Elevated growth hormone levels in stunted Atlantic salmon, *Salmo salar*. Aquaculture 73: 275–281.

Bolton, J. P., A. Takahashi, H. Kawauchi, J. Kubota, and T. Hirano. 1986. Development and validation of a salmon growth hormone radioimmunoassay. Gen. Comp. Endocrinol. 62: 230–238.

Bolton, J. P., G. Young, R. S. Nishioka, T. Hirano, and H. A. Bern. 1987. Plasma growth hormone levels in normal and stunted yearling coho salmon, *Oncorhynchus kisutch*. J. Exp. Zool. 242: 379–382.

Clarke, W. C., and Y. Nagahama. 1977. Effects of premature transfer to sea water on juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 55: 1620–1630.

Donaldson, E. M. 1981. The pituitary–interrenal axis as an indicator of stress in fish, p. 11–48. *In* A. D. Pickering [ed.] Stress and fish. Academic Press, New York, NY.

Folmar, L. C., and W. W. Dickhoff. 1980. The parr–smolt transformation (smoltification) and seawater adaptation in salmonids. A review of selected literature. Aquaculture 21: 1–37.

Folmar, L. C., W. W. Dickhoff, C. V. W. Mahnken, and F. W. Waknitz. 1982. Stunting and parr-reversion during smoltification of coho salmon (*Oncorhynchus kisutch*). Aquaculture 28: 91–104.

Fryer, J. N., and H. A. Bern. 1979. Growth hormone binding to tissues of normal and stunted juvenile coho salmon, *Oncorhynchus kisutch*. J. Fish Biol. 15: 527–533.

Gorbman, A., W. W. Dickhoff, J. L. Mighell, E. F. Prentice, and F. W. Waknitz. 1982. Morphological indices of developmental progress in the parr–smolt coho salmon, *Oncorhynchus kisutch*. Aquaculture 28: 1–19.

Gray, E. S., G. Young, and H. A. Bern. 1990. Radioreceptor assay for growth hormone in coho salmon (*Oncorhynchus kisutch*) and its application to the study of stunting. J. Exp. Zool. 256: 290–296.

Hoar, W. S. 1988. The physiology of smolting salmonids, p. 275–343. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. XIB. Academic Press, San Diego, CA.

Kubo, T. 1974. Notes on the phase differentiation and smolt transformation of juvenile masu salmon (*Oncorhynchus masou*). Sci. Rep. Hokkaido Salmon Hatchery No. 28: 17 p.

Leatherland, J. F. 1985. Studies of the correlation between stress-response, osmoregulation and thyroid physiology in rainbow trout, *Salmo gairdneri* (Richardson). Comp. Biochem. Physiol. A 80: 523–531.

Mahnken, C. V. W., A. J. Novotny, and T. Joyner. 1970. Salmon mariculture potential assessed. Am. Fish Farm. 2(1): 12–15.

Marini, G., and T. H. Kerstetter. 1982. Intracellular electrolyte regulation in freshwater and seawater adapted coho salmon. Aquaculture 28: 75–80.

Nishioka, R. S., H. A. Bern, K. V. Lai, Y. Nagahama, and E. G. Grau. 1982. Changes in endocrine organs of coho salmon during normal and abnormal smoltification — an electron microscope study. Aquaculture 28: 21–38.

Pickering, A. D., T. G. Pottinger, J. P. Sumpter, J. F. Carragher, and P. Y. Le Bail. 1991. Effects of acute and chronic stress on the levels of circulating growth hormone in the rainbow trout, *Oncorhynchus mykiss*. Gen. Comp. Endocrinol. 83: 86–93.

Redding, J. M., C. B. Schreck, E. K. Birks, and R. D. Ewing. 1984. Cortisol and its effects on plasma thyroid hormone and electrolyte concentrations in fresh water and during seawater acclimation in yearling coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrinol. 56: 146–155.

Sakamoto, T., M. Iwata, and T. Hirano. 1991. Kinetic studies of growth hormone and prolactin during adaptation of coho salmon, *Oncorhynchus kisutch*, to different salinities. Gen. Comp. Endocrinol. 81: 184–191.

Specker, J. L., and L. Kobuke. 1987. Seawater-acclimation and thyroidal response to thyrotropin in juvenile coho salmon (*Oncorhynchus kisutch*). J. Exp. Zool. 241: 327–332.

Sweeting, R. M., G. F. Wagner, and B. A. McKeown. 1985. Changes in plasma glucose, amino acid nitrogen and growth hormone during smoltification and seawater adaptation in coho slmon, *Oncorhynchus kisutch*. Aquaculture 45: 185–197.

Tagawa, M., and T. Hirano. 1987. Presence of thyroxine in eggs and changes in its content during early development of chum salmon, *Oncorhynchus keta*. Gen. Comp. Endocrinol. 68: 129–135.

1990. Changes in tissue and blood concentrations of thyroid hormones in developing chum salmon. Gen. Comp. Endocrinol. 76: 437–443.

Takahashi, A., J. Kubota, H. Kawauchi, and T. Hirano. 1985. Effects of *N*-terminal peptide of salmon proopiocortin on interrenal function of the rainbow trout. Gen. Comp. Endocrinol. 58: 328–335.

Varnavsky, V. S. 1989. Smoltification of salmon. DVO AN USSR, Vladivostok. 150 p.

Young, G. 1985. In vitro studies on interrenal gland activity during smoltification of coho salmon. Aquaculture 45: 391–392.

Young, G., B. Th. Björnsson, P. Prunet, R. J. Lin, and H. A. Bern. 1989a. Smoltification and seawater adaptation in coho salmon (*Oncorhynchus kisutch*): plasma prolactin, growth hormone, thyroid hormones, and cortisol. Gen. Comp. Endocrinol. 74: 335–345.

Young, G., P. Prunet, T. Ogasawara, T. Hirano, and H. A. Bern. 1989b. Growth retardation (stunting) in coho salmon: plasma hormone levels in stunts in seawater and after transfer to fresh water. Aquaculture 82: 269–278.

Deep Diving in Wild, Free-Ranging Beluga Whales, *Delphinapterus leucas*

A. R. Martin

Sea Mammal Research Unit, c/o British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, U.K.

and T. G. Smith[1]

Department of Fisheries and Oceans, Arctic Biological Station, 555 Boulevard St-Pierre, Ste-Anne-de-Bellevue (Québec) H9X 3R4, Canada

Martin, A. R., and T. G. Smith. 1992. Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas*. Can. J. Fish. Aquat. Sci. 49: 462–466.

Three adult female beluga whales, *Delphinapterus leucas*, were captured during summer in the Canadian high Arctic and equipped with satellite-linked radio transmitters that measured and recorded ambient pressure every 20 s. Diving behaviour was divisible into three distinct categories: (1) near-surface, (2) "spike" dives to 20–150 m depth, and (3) prolonged, flat-bottomed dives to a maximum depth of 350 m. The duration of these prolonged dives was 9.3–13.7 min, but the upper bound is known to be underestimated. Average descent rates varied between dives in the range 1.43–2.20 m/s and ascent rates between 1.23 and 1.84 m/s. Within periods of 20 s duration, maximum descent and ascent rates were 2.55 and 2.35 m/s, respectively. After most prolonged dives the rate of ascent declined progressively as the surface was approached, particularly in the final 100 m. Such dives were usually to, or near to, the seabed and were probably for foraging. Up to 42% of an animal's time could be spent at depths of 8 m or more.

Le comportement de plongée de trois femelles belugas adultes, *Delphinapterus leucas*, a été étudié durant l'été. Nous les avons capturées dans le haut arctique canadien et avons placé, sur leur dos, des émetteurs satellites capables de mesuré la pression ambiante à une fréquence de 20 s. Le comportement de plongée se divise en trois catégories distinctes : (1) plongées à proximité de la surface, (2) plongées "verticales aller-retour" de 20–150 m et (3) plongées de plus longue durée, à profil plat — avec déplacement horizontal — allant jusqu'à une profondeur maximale de 350 m. La durée calculée des plongée à longue durée est de 9,3 à plus de 13,7 min. Les taux moyens de descente variaient entre 1,43 et 2,20 m/s et ceux d'ascension entre 1,23 et 1,84 m/s. Durant des périodes de durée de 20 s, les taux maximums de descente et d'ascension étaient de 2,55 et 2,35 m/s respectivement. Après des plongées de longue durée, le taux d'ascension ralentissait en approchant la surface, particulièrement dans les derniers 100 m. Les belugas en plongée se rendaient normalement près ou jusqu'au fond, vraisemblablement pour des fins d'alimentation. Jusqu'à 42 % du budget horaire d'un béluga peut être passé à des profondeurs de 8 m ou plus.

Received July 3, 1991
Accepted October 4, 1991
(JB111)

Reçu le 3 juillet 1991
Accepté le 4 octobre 1991

Very little is known about the diving behaviour of cetaceans. For logistical, financial, and technological reasons it has proven very difficult to gain information on the underwater activity of a group of animals which are totally aquatic, large in body size, and fast-swimming. Ridgway (1986) reviewed the published accounts of the depth and duration of dives of cetaceans and found information on 10 species. Of these, five were known only from studies of captive animals, two from indirect behavioural evidence, one from measurements on a harpooned whale, and only two from studies of wild, unrestrained animals. These two are the sperm whale (*Physeter macrocephalus*) (Norris and Harvey 1972; Gordon 1987; Mullins et al. 1988; Papastavrou et al. 1989) and the common dolphin (*Delphinus delphis*) (Evans 1971).

The published evidence for diving behaviour of the beluga, *Delphinapterus leucas*, suggests contradictions. Field studies report dives to 20 m or less (Tomilin 1957; Kleinenberg et al. 1964), yet studies of trained belugas in the open sea have demonstrated a physiological capability of diving to about 650 m and for up to 16 min (Ridgway et al. 1984). The stomachs of freshly dead belugas have often contained organisms which could only have been obtained from the seabed (Klumov and Dorofeev 1936; Vladikov 1947; Kleinenberg et al. 1969), but whether this food was gathered in shallow or deep water could not be determined.

To examine the diving behaviour of wild, free-ranging belugas, we equipped three animals with small electronic devices which would allow accurate determination of their geographical location and provide detailed dive profile data.

Materials and Methods

Belugas were captured by driving them into shallow water along the shore of Cunningham Inlet, N.W.T., Canada (74°05′N, 93°45′W). The selected animals were restrained by first placing a hoop net over their heads and around their pectoral fins. Once captured they were further secured by tying a rubber covered rope around the caudal peduncle and anchoring it on shore. The animal could then be restrained with just the dorsal surface above water by one person sitting on its back.

---

[1] Current address: Department of Fisheries and Oceans, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, B.C. V9R 5K6, Canada.

Three female beluga whales were equipped with back-mounted electronic packages comprising a UHF radio transmitter (Toyocom Ltd., Tokyo, Japan), a microprocessor, and pressure and emergence sensors. The units were powered by lithium thionyl chloride batteries and housed in tubes of anodised aluminium, capable of withstanding pressures equivalent to a water depth in excess of 2000 m. They were attached to the dorsal ridge of the animals by means of a ''saddle'' of pliable material, and three 4.5-mm-diameter nylon pins which migrate out of the tissue after a period of weeks, releasing the package. One transmitter was deployed at Cunningham Inlet in the summer of 1989 and the other two in 1990.

Signals from the transmitters were received by polar-orbit NOAA satellites and relayed to the laboratory via System Argos, based in Toulouse, France. When certain operational conditions are met, System Argos permits the geographical location of transmitters to be determined to an accuracy of better than 1 km during a satellite ''pass'' (Fancy et al. 1988; Keating et al. 1991). Such passes occur more than 20 times per day at the high latitudes at which this study was carried out. In addition to locational data, information on ambient pressure was collected and relayed by satellite. Pressure was measured every 20 s continuously and, at each transmission, the last 32 pressure measurements were relayed, giving the depth of the animal during the 10.3 min immediately prior to surfacing. With this protocol, depth data were collected for approximately 23% of the period during which a transmitter was functioning, spread throughout the 24-h period but with a greater coverage during daylight hours. Accuracy of these measurements, checked by repeated ''cycling'' to maximum depth in a barometric pressure chamber, was to approximately ±2.5 m of the true depth down to 650 m. Water depths at known locations of the study animals were determined from the appropriate chart issued by the Canadian Hydrographic Service.

Results

All three transmitters were attached to adult female belugas, measuring 291–416 cm in body length. Transmitter No. 5802 was deployed at 17:33 local time on 27 July 1989. Signals were received locally for about 30 min while the animal swam out of Cunningham Inlet, but only one useful dive profile was subsequently received by the satellite. This dive was completed at 17:21 local time on 3 August at an unknown location, but in deep water, as the maximum dive depth was 321 m.

Transmitter No. 5801 was placed on an animal at 13:07 local time on 17 July 1990 and functioned correctly for 8 d. The whale moved out of Cunningham Inlet after release and spent the entire period of transmitter operation in deep water in Barrow Strait, in depths of 150–350 m.

Transmitter No. 5803 was deployed at 15:36 local time on 18 July 1990 and functioned correctly for 11 d. The animal remained within Cunningham Inlet, in water depths of 40 m or less, for the first 5 d after capture and then headed north, west, and south into Barrow Strait and Peel Sound, remaining in waters of 150–270 m depth for the final period of transmitter operation.

Subsurface activity of the three study animals could be divided into three recognisable categories: (1) near-surface, with surfacings at intervals of 1 min or less, i.e. dives of short duration, (2) ''spike'' dives of 4 min or less, comprising a descent to 20–150 m depth with an immediate return to the surface, and (3) prolonged, flat-bottomed dives to depths of 20–350 m. In this paper, we will consider in detail only these prolonged dives and, in particular, those to a depth of 100 m or more. These were of a very characteristic ''square'' profile,

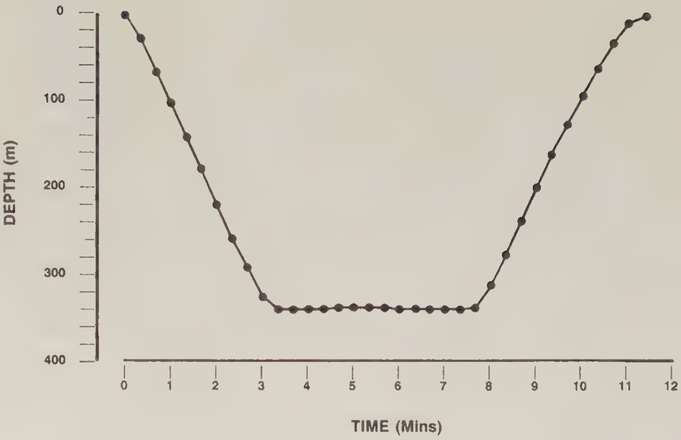


FIG. 1. Typical profile of the type of deep dives described in this paper. This dive (No. 146 of beluga No. 5801) had an estimated bottom time of 4.1 min, a mean descent rate of 1.88 m/s, and an ascent rate decreasing from 1.95 to 1.15 m/s. It was carried out at 19:15 local time on 21 July 1990 in water of approximately 335 m depth at position 74°14′N, 90°59′W.

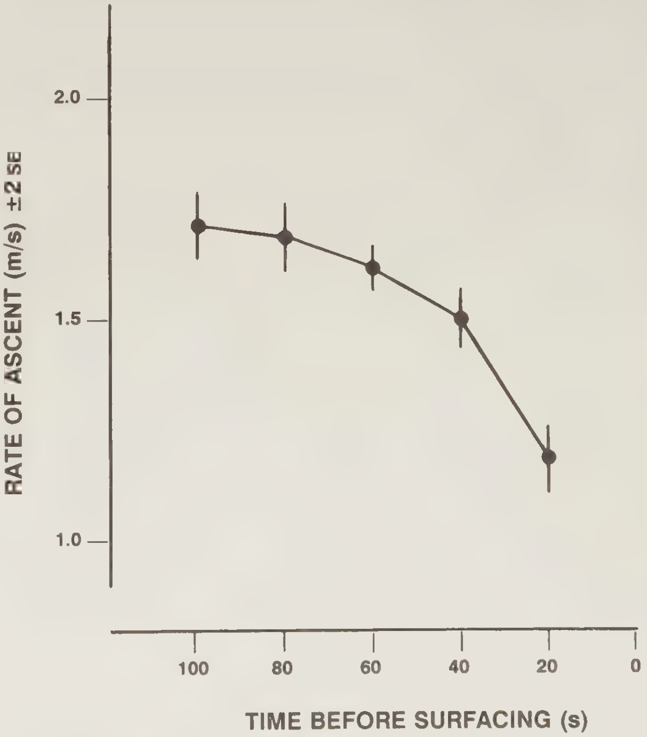


FIG. 2. Rate of ascent as the surface is approached after a deep dive (n = 39). Values represent the average rate over consecutive periods of 20 s. The right-most point is that of the final complete 20-s interval measured before surfacing, which ended randomly at any time between 0.1 and 19.9 s before the animal surfaced. The value on the horizontal axis for each point therefore represents the approximate midpoint of each consecutive interval.

with an almost linear rate of descent, a period of several minutes spent at a constant depth, and an ascent which often slowed progressively as the surface was neared, particularly in the final 100 m (Fig. 1 and 2).

The whales normally surfaced very near the point of submergence after these deep dives. Estimated dive duration was in the range 560–820 s (9.3–13.7 min) including, where necessary, an extrapolation for any part of the descent which was not recorded within the 620-s ''window'' of the transmitter. The duration of 23% of dives could not be estimated because the entire descent was missed. Some of these dives were probably longer than 820 s, but the shape of the frequency distribution of known dive durations suggests that few exceed this limit. The mean duration of 39 dives to 150 m or more was 686 s (11.4 min), but this is an underestimate based on the assumption that no part of the constant depth ''bottom'' segment of the nine incomplete dive profiles (see Fig. 1) had been missed. The regression of maximum depth of the dive on dive duration was significant and positive ($n = 36$, $r^2 = 0.53$, $p < 0.001$).

The rate of descent, averaged over the entire descent, was in the range of 1.43–2.20 m/s. Average ascent rates varied between 1.23 and 1.84 m/s over the entire ascent, but the rate of vertical movement progressively diminished as the surface was approached. In dives to 150 m depth or more, the rate of ascent (expressed as an average over each consecutive period of 20 s) fell from 1.71 m/s about 100 s before reaching the surface (equivalent to a depth of about 140 m) to 1.18 m/s in the last complete interval before surfacing (Fig. 2). Over periods of 20 s, the maximum recorded rates of descent and ascent were 2.55 and 2.35 m/s, respectively. Regression of the average rate of ascent on the duration and maximum depth of the dive was significant and positive ($n = 36$, $r^2 = 0.37$, $p < 0.001$ and $n = 40$, $r^2 = 0.43$, $p < 0.001$, respectively). There was no significant relationship between the average rate of descent and either dive duration or depth.

Measured ''bottom'' time, the period spent at constant depth after the descent, was in the range 180–420 s (3–7 min), typically representing 45–60% of the total period of submergence. The upper time limit is almost certainly an underestimate because, as mentioned above, the end of the descent phase and beginning of the period at maximum depth was not recorded for nine of the longer dives.

The length of time spent at or near the surface between deep dives was rarely recorded because the recording ''window'' was too short. Nevertheless, it was estimated on three occasions to be approximately 6 min between dives of about 13 min duration, once to be 4 min between dives of at least 9 min, and once to be 1 min between dives of 4 and 5 min. The proportion of time overall spent at or near the surface varied dramatically according to the behaviour of the whales and, in particular, whether they were engaged in bouts of prolonged dives. Whale No. 5803 spent five consecutive days in the shallow waters of Cunningham Inlet and rarely ventured to depths of more than a few metres throughout this time. In contrast, animal No. 5801, on 22 July 1990 during a period of intensive deep diving, was estimated to spend 42% of the 24-h period at a depth of 8 m or more (Fig. 3).

All deep dives recorded for female No. 5801 were carried out, as accurately as it was possible to measure, to the seabed or very near to it in water depths of 170–350 m. The one dive recorded for female No. 5802 was to a depth of 321 m. Although the location at which this dive was made, and therefore the water depth, was not known, there is so little water within range deeper than 300 m and none deeper than 350 m, that this dive must also have been to or near the seabed. Whale No. 5803 carried out ''square'' profile dives both in midwater and to the seabed. In water depths of 200 ± 30 m, this animal made many dives of 6–10 min duration but only to 15–25 m below the water surface.

Discussion

These results demonstrate, contrary to Klumov and Dorofeev (1936) and Kleinenberg et al. (1964), that wild belugas may routinely dive to considerable depths. Indeed, the small area in which female No. 5801 spent a period of almost 4 d diving to 300 m or more is the only one in Barrow Strait where such depths exist. The fact that two of three additional belugas which were equipped with location-only transmitters (providing no depth information) during July 1990 also spent several days in this same area suggests that it was a popular locality for this stock of whales, at least in that year.

We assume that the function of deep dives in this species is that of foraging. Animal No. 5801, and the two other belugas we know to have spent time in the area of the deepest water, moved very little distance horizontally, so there seems to be no link to travelling. This activity also occurred well ahead of the annual autumn migration of belugas to the east. We know from direct observation and our telemetry data that the periods of fastest horizontal movements are characterised by shallow dives.

If our assumption is correct and deep dives are carried out for foraging, then the periods of continuous diving (see Fig. 3) indicate intensive feeding in offshore areas, supporting previous conclusions that belugas sampled in or near estuaries are not feeding in these shallow-water areas during summer months (Sergeant 1973; Fraker et al. 1979; Brodie 1989; Reeves and Mitchell 1987; Caron 1987; Doidge 1990). Significantly, an ability to dive to 350 m allows belugas access to most of the benthic production in the Arctic Ocean.

There is very little information about the identity, distribution, or abundance of potential prey species at these depths in the Canadian high Arctic. Arctic cod (*Boreogadus saida*), a common prey of belugas and other Arctic marine mammals, is widely distributed and relatively abundant throughout nearby Lancaster Sound (Bradstreet et al. 1986). In hydroacoustic surveys of Lancaster Sound, Crawford and Jorgenson (1990) did find what they assumed to be Arctic cod at depths of >400 m, but not usually in significant quantities below 200 m. The highest densities were located immediately below the ice layer which was present during their surveys. The assumption that most of their target echoes were of Arctic cod was based on the lack of direct evidence of any other species in their study area, but we must consider the possibility that there are other prey species present. Greenland halibut (*Reinhardtius hyperglossoides*), which lives on or near the bottom in deep water (Bigelow and Welsh 1924; Scott 1982; Hudon 1990) and is patchy in its distribution (Atkinson and Bowering 1987), is possibly taken by belugas in the deepwater areas of Barrow Strait sought by the whales in this study. From the examination of hunter-killed belugas, other prey might include shrimp, crabs, or other invertebrates, many of these available only on or near the seabed (Tomilin 1957; Brodie 1989).

Rates of descent and ascent are similar to those for seals (e.g. Kooyman 1989; Le Boeuf et al. 1989) and within the range

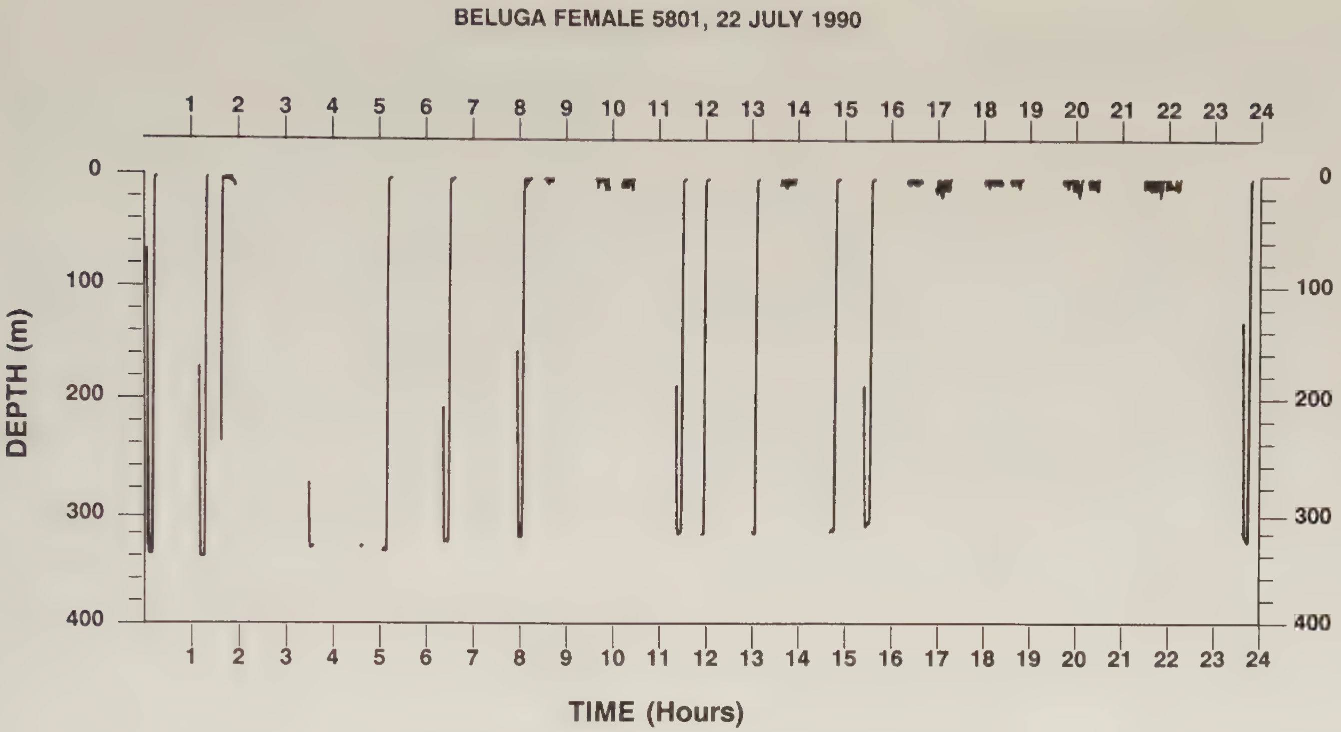


FIG. 3. Plot of depth against time for beluga No. 5801 on 22 July 1990.

reported for trained belugas (Ridgway et al. 1984). The progressive slowing of the ascent rate within about 140 m of the surface (Fig. 1 and 2) has not been previously reported, perhaps because the resolution allowed by the method of data collection was not sufficiently fine. Nevertheless, it is a characteristic of nearly all the deep dives we recorded for animal No. 5801 and may have a physiological function, perhaps to reduce the rate at which gas bubbles appear in blood or tissues as the ambient pressure diminishes. Since expansion of gas in the lungs and other air passages must progressively increase the buoyancy of the animal as it moves to the surface, the observed slowing of the rate of ascent must occur because of a reduction in swimming speed, a flattening of trajectory, or both.

The discovery that wild beluga whales may remain underwater for periods of 13 min or more, and for up to 42% of any 24-h period, has important implications for the interpretation of survey results. At least in deep water, all three of our study animals spent a substantial proportion of time well below the surface and would probably have been missed by observers aboard a ship or aircraft. Although large numbers of high Arctic belugas are commonly seen in bays and estuaries, or within 500 m of the coast in summer, this study supports the findings of Smith et al. (1985) and Richard et al. (1990) that a significant proportion of the stock occurs offshore. Future surveys should employ a correction factor for those animals estimated to be out of sight when the observation platform passed. In coastal waters, visual observations from land may be sufficient to allow the calculation of an appropriate correction factor (Brodie 1971), but similar information for animals offshore can only realistically be gathered using radio telemetry.

Acknowledgements

We are indebted to the Polar Continental Shelf Project (PCSP) for generous logistical support and WWF-UK for financial help. We thank Gilly Banks, Kathy Frost, Haakon Hop, George Horonowitsch, and Gary Sleno for invaluable field or logistical support and Oliver Cox, Charlie Chambers, Ailsa Hall, Colin Hunter, Bernie McConnell, Kevin Nicholas, Jeremy Tomlinson, and Last Engineering for help with preparation of the transmitters or data analysis. Drs. Mike Fedak and Sam Ridgway provided welcomed guidance on the interpretation of the results. Mimi Breton kindly provided the French translation of the abstract.

References

ATKINSON, D. B., AND W. R. BOWERING. 1987. The distribution and abundance of Greenland halibut, deep water redfish, golden redfish, roundnose grenadier and roughhead grenadier in Davis Strait. Can. Tech. Rep. Fish. Aquat. Sci. 1578: v + 29 p.

BIGELOW, H. B., AND W. W. WELSH. 1924. Bulletin of the U.S. Bureau of Fisheries, 965: Fishes of the Gulf of Maine. Vol. XL. Part I. Government Printing Office, Washington, DC. 567 p.

BRADSTREET, M. S. W., K. J. FINLEY, A. D. SEKERAK, W. B. GRIFFITHS, C. R. EVANS, M. F. FABIJAN, AND H. E. STALLARD. 1986. Aspects of the biology of Arctic cod (*Boreogadus saida*) and its importance in Arctic marine food chains. Can. Tech. Rep. Fish. Aquat. Sci. 1491: 193 p.

BRODIE, P. F. 1971. A reconsideration of aspects of growth, reproduction and behaviour of the white whale (*Delphinapterus leucas*) with reference to the Cumberland Sound, Baffin Island, population. J. Fish. Res. Board Can. 28: 1309–1318.

1989. The white whale — *Delphinapterus leucas*. *In* S. H. Ridgway and R. J. Harrison [ed.] Handbook of marine mammals. Vol. 4: River dolphins and the larger toothed whales. Academic Press Limited, London and San Diego.

CARON, M. J. 1987. Status, site fidelity and behaviour of a hunted herd of white whales (*Delphinapterus leucas*) in the Nastapoka estuary, eastern Hudson Bay. M.Sc. thesis, McGill University, Montreal, Que.

CRAWFORD, R., AND J. JORGENSON. 1990. Density distribution of fish in the presence of whales at the Admiralty Inlet land-fast ice edges. Arctic 43: 215–222.

DOIDGE, D. W. 1990. Age and stage based analysis of the population dynamics of beluga whales, *Delphinapterus leucas*, with particular reference to the northern Quebec population. Ph.D. thesis, McGill University, Montreal, Que.

Evans, W. E. 1971. Orientation behaviour of delphinids: radio telemetric studies. Ann. N.Y. Acad. Sci. 188: 142–160.

Fancy, S. G., L. F. Pank, D. G. Douglas, C. H. Curby, G. W. Garner, S. C. Amstrup, and W. L. Regelin. 1988. Satellite telemetry: a new tool for wildlife research and management. U.S. Dep. Interior, U.S. Fish Wildl. Serv. Resour. Publ. 172.

Fraker, M. A., C. D. Gordon, J. W. McDonald, J. K. B. Ford, and G. Cambers. 1979. White whale (*Delphinapterus leucas*) distribution and abundance and the relationship to physical and chemical characteristics of the Mackenzie Estuary. Can. Fish. Mar. Serv. Tech. Rep. 863: 1–36.

Gordon, J. C. D. 1987. Behaviour and ecology of sperm whales off Sri Lanka. Ph.D. thesis, University of Cambridge, Cambridge, U.K.

Hudon, C. 1990. Distribution of shrimp and fish by-catch assemblages in the Canadian eastern Arctic in relation to water circulation. Can. J. Fish. Aquat. Sci. 47: 1710–1723.

Keating, K. A., W. G. Brewster, and C. H. Key. 1991. Satellite telemetry: performance of animal-tracking systems. J. Wildl. Manage. 55: 160–171.

Kleinenberg, S. E., A. V. Yablokov, V. M. Belkovich, and M. N. Tarasevich. 1964. Beluga *Delphinapterus leucas*. Investigations of the species. Nauka, Moscow. 131 p. (English translation, Israel Program for Scientific Translation, Jerusalem)

Klumov, S. K., and S. V. Dorofeev. 1936. Promyslovya Kharakteristiki migratsii belukhi v raione ostrova Sakhalina (Commercial characteristics of the migration of the beluga in Sakhalin waters). Tr. VNIRO 3.

Kooyman, G. L. 1989. Diverse divers: physiology and behaviour. Vol. 23. Springer-Verlag, Berlin. 200 p.

Le Boeuf, B. J., Y. Naito, A. C. Huntley, and T. Asaga. 1989. Prolonged, continuous, deep diving by northern elephant seals. Can. J. Zool. 67: 2514–2519.

Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. Can. J. Fish. Aquat. Sci. 45: 1736–1743.

Norris, K. S., and G. W. Harvey. 1972. A theory of the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.). *In* S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, and R. E. Belleville [ed.] Animal orientation and navigation. NASA, Washington, DC.

Papastavrou, V., S. C. Smith, and H. Whitehead. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. Can. J. Zool. 67: 839–846.

Reeves, R. R., and E. Mitchell. 1987. Distribution and migration, exploitation, and former abundance of white whales *Delphinapterus leucas* in Baffin Bay and adjacent waters. Can. Spec. Publ. Fish. Aquat. Sci. 99: 34 p.

Richard, P., J. R. Orr, and D. G. Barber. 1990. The distribution and abundance of belugas, *Delphinapterus leucas*, in eastern Canadian subarctic waters: a review and update. *In* T. G. Smith, D. J. St. Aubin, and J. R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224.

Ridgway, S. H. 1986. Diving by cetaceans. *In* A. O. Brubakk, J. W. Kanwisher, and G. Sundnes [ed.] Diving in animals and man. Royal Norwegian Society of Sciences and Letters, Trondheim, Norway.

Ridgway, S. H., C. A. Bowers, D. Miller, M. L. Schultz, C. A. Jacobs, and C. A. Dooley. 1984. Diving and blood oxygen in the white whale. Can. J. Zool. 62: 2349–2351.

Scott, J. S. 1982. Depth, temperature and salinity preferences of common fishes of the Scotian Shelf. J. Northwest Atl. Fish. Sci. 3: 29–39.

Sergeant, D. E. 1973. Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. J. Fish. Res. Board Can. 30: 1065–1090.

Smith, T. G., M. O. Hammill, D. J. Burrage, and G. A. Sleno. 1985. Distribution and abundance of belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, in the Canadian high Arctic. Can. J. Fish. Aquat. Sci. 42: 676–684.

Tomilin, A. G. 1957. Mammals of the USSR and adjacent countries: cetacea. Nauk USSR, Moscow. (English translation, Israel Program for Scientific Translations, Jerusalem)

Vladikov, V.-D. 1947. Études sur les mammifères aquatiques. IV — Nourriture du marsouin blanc ou beluga (*Delphinapterus leucas*) du fleuve Saint-Laurent. Contrib. Inst. Biol. Zool. 19: 129.

Larval Flatfish Distributions and Drift on the Southern Grand Bank

Kenneth T. Frank and John W. Loder

Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2, Canada

James E. Carscadden

Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, Nfld. A1C 5X1, Canada

William C. Leggett

Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, Que., H3A 1B1, Canada

and Christopher T. Taggart

Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, Nfld. A1C 5X1, Canada

Frank, K. T., J. W. Loder, J. E. Carscadden, W. C. Leggett, and C. T. Taggart. 1992. Larval flatfish distributions and drift on the southern Grand Bank. Can. J. Fish. Aquat. Sci. 49: 467–483.

Ichthyoplankton and hydrographic surveys of the southern Grand Bank in September of 1986, 1987, and 1988 revealed substantial correspondence between the areal distributions of larvae of three flatfish species and temperature below the thermocline. Depth-averaged densities of American plaice (*Hippoglossoides platessoides*) were negatively correlated with temperature whereas yellowtail flounder (*Limanda ferruginea*) and witch flounder (*Glyptocephalus cynoglossus*) densities were positively correlated with temperature. In spite of large interannual differences in abundance, the larval distributions showed similar structure from year to year. Using estimates of larval age inferred from length frequency distributions and literature values for growth rate, in conjunction with moored current measurements, estimates of spawning times and locations were obtained for each species. These estimates were compared with historical information on the distribution of prespawning fish for each species to examine the hypothesis of passive larval drift. The results indicate that in most, but not all cases, the larval distributions and currents are consistent with passive larval drift for particular growth rates and vertical distributions. However, the observations are not adequate to rule out alternative mechanisms involving behaviour.

Des relevés de l'ichtyoplancton et des paramètres hydrographiques effectués dans le secteur sud des Grands Bancs en septembre 1986, 1987 et 1988 ont révélé une correspondance importante entre la répartition spatiale des larves de trois espèces de poissons plats et la température de l'eau sous la thermocline. Les densités, en fonction de la moyenne des profondeurs, des larves de plie canadienne (*Hippoglossoides platessoides*) étaient en corrélation négative avec la température, tandis que les densités de larves de limande à queue jaune (*Limanda ferruginea*) et de plie grise (*Glyptocephalus cynoglossus*) étaient en corrélation positive avec cette variable. Malgré d'importantes différences inter-annuelles de l'abondance, la répartition des larves présentaient une structure semblable d'une année à l'autre. À l'aide d'estimations de l'âge des larves établies à partir des distributions de la fréquence des longueurs, de taux de croissance tirés d'ouvrages publiés et de quantifications courantométriques, les auteurs ont obtenu des estimations du moment et du lieu de la fraie de chaque espèce. Ils ont ensuite comparé ces estimations à des données historiques sur la répartition de chaque espèce avant la fraie pour tenter d'étayer l'hypothèse d'une dérive passive des larves. Les résultats révèlent que dans la plupart des cas, mais pas tous, la répartition des larves et les courants appuient cette hypothèse dans le cas de certains taux de croissance et de répartition verticale. Toutefois, les observations ne suffisent pas à écarter d'autres mécanismes liés au comportement.

Received December 21, 1990
Accepted October 10, 1991
(JA845)

Reçu le 21 décembre 1990
Accepté le 10 octobre 1991

A common approach in investigations aimed at understanding recruitment to marine fish populations and its variability is a search for and quantification of the factors that determine the distribution and survival of the early life stages. Hypotheses include those in which purely environmental factors such as water drift (or lack thereof) dominate (e.g. Myers and Drinkwater 1988) and those requiring significant behavioural components such as vertical migration in relation to currents (e.g. Sinclair 1988). The possibility of retention, or an extended residence time in a particular area, has been suggested for many species and has been attributed both to purely physical processes (e.g. American plaice (*Hippoglossoides platessoides*), Nevinsky and Serebryakov 1973; silver hake (*Merluccius bilinearis*), Fahay 1974) and vertical migration in relation to depth-varying currents (e.g. Atlantic herring (*Clupea harengus harengus*), Sinclair and Iles 1988).

Two physical factors that affect the degree to which eggs and larvae are retained within an area are its horizontal extent and the rate of horizontal water exchange. Together, these factors determine the water residence time (extent/exchange rate). The Grand Bank of Newfoundland, a continental shelf region used as a spawning ground by numerous species, has both a broad plateau and weak subtidal currents (except in the Labrador Current around its perimeter) (e.g. Petrie and Anderson 1983; Loder et al. 1988). Therefore, retention of early life stages might be expected to be a common feature on the Bank.

In this paper we report the distributions of the early life stages of three flatfish species on the southern Grand Bank, as observed in ichthyoplankton surveys conducted in September of 1986, 1987, and 1988. The species examined are American plaice, yellowtail flounder (*Limanda ferruginea*), and witch flounder (*Glyptocephalus cynoglossus*). There is limited information on the distribution of larvae and juveniles of these species in the area. However, extensive sampling of older juveniles (ages 1 and older), conducted since 1985, indicates that the southern Bank may be a juvenile nursery area for yellowtail and plaice (Walsh 1991). We describe the distributions of larvae and 0-group juveniles in relation to the temperature field and use current measurements derived from moored instruments to estimate their movement and probable spawning sites, assuming that the dominant influence is water drift. We use the results of these analyses to assess the hypothesis that passive drift from spawning areas can account for the observed larval distributions.

Materials and Methods

Study Area

The study area (Fig. 1) was the Southeast Shoal (approximate centre 44°30′N, 50°W) of the Grand Bank, its

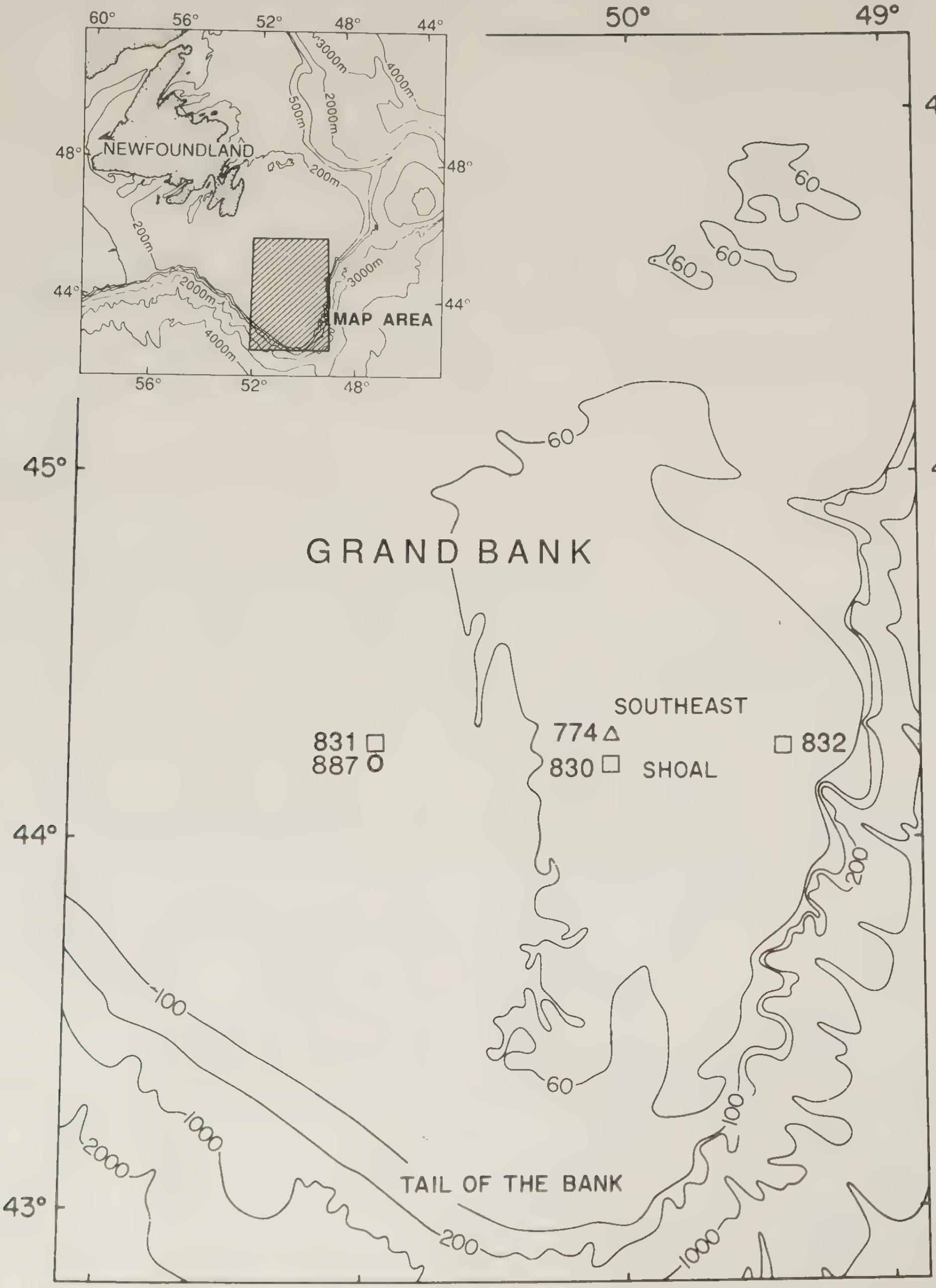

60°
56°
52°
48°
44°
3000m
4000m
500m
2000m
48°
NEWFOUNDLAND
200m
48°
200m
3000m
44°
2000m
44°
MAP AREA
4000m
56°
52°
48°
50°
49°
46°
60
60
60
60
45°
45°
GRAND BANK
SOUTHEAST
831 □
887 ○
774 △
830 □
SHOAL
□ 832
44°
44°
200
100
60
100
1000
2000
TAIL OF THE BANK
43°
43°
200
1000
52°
51°
50°
49°

FIG. 1. Location map for the southern Grand Bank with the 1986–88 current meter mooring sites (see Table 1 for times and depths). △, 1986; □, 1987; ○, 1988.

TABLE 1. Summary of positions, depths (below surface), and periods with reliable data for current meter measurements on the southern Grand Bank in 1986–88. Mooring No. refers to the Bedford Institute of Oceanography Consecutive Number.

Mooring No.	Latitude (N)	Longitude (W)	Water depth (m)	Instrument depth (m)	Data return period (calendar days)
1986					
774	44°14.4′	50°04.2′	55	20	108–215
				45	108–268
1987					
830	44°16.0′	50°05.3′	54	11	123–275
				44	123–257
831	44°14.9′	50°58.8′	72	14	123–292
				47	123–292
832	44°13.3′	49°19.5′	55	12	124–187
				45	124–291
1988					
887	44°15.1′	50°59.9′	73	13	121–262
				63	121–262

shallowest area. The Shoal is or has been the site of major domestic and international fisheries for capelin, cod, and flatfishes. It is a major spawning area for capelin and has been the site of studies on spawning (Carscadden et al. 1989) and early life stages (Frank and Carscadden 1989) of capelin and on juvenile stages of flatfish (Walsh 1991). The principal features of its spring–fall physical oceanographic regime are an approximate two-layer stratification (e.g. Loder 1991), weak subtidal currents, and a branch of the Labrador Current along the shelf break to the east (e.g. Petrie and Anderson 1983).

Physical Oceanography

The current and hydrographic fields in the Southeast Shoal region were monitored in 1986, 1987, and 1988 using moored sensors deployed from spring to fall (Ross et al. 1988) and hydrographic surveys. The returned data include time series from two Aanderaa current meters at each of one site in 1986, three sites in 1987, and one in 1988 (see Fig. 1 and Table 1, and Ross et al. 1988 for details). Temperature and salinity distributions were obtained during the 1986–88 September larval surveys from a CTD mounted on the BIONESS net system (Sameoto et al. 1980) and from XBT casts. Temperature and salinity data for other times during spring–fall of 1986–88 were obtained from dedicated hydrographic (CTD and XBT) surveys and from the Marine Environmental Data Service (MEDS). The MEDS data were screened for suspect values which were removed, and all the hydrographic data were subsequently grouped into time intervals of 1–2 wk duration which provided quasi-synoptic coverage of the region.

Adults

Spawning has never been directly observed for any of the three species studied. Published historical accounts of adult distributions, the approximate limits of the distribution of prespawners, and the relationship between these prespawning distributions and bottom temperatures were therefore used to a delimit the expected spawning times and locations.

Larvae and Juveniles (0-Group)

The sampling methods used are detailed in Frank and Carscadden (1989). Briefly, the horizontal and vertical distributions of larvae of the three flatfish species were assessed from surveys conducted in September of 1986, 1987, and 1988. In 1986, a rectangular grid of 39 stations spaced at 10 nautical mile intervals along six transects was sampled. Eight additional stations were sampled along 44°15′ centered on the shelf break. In 1987 the grid was expanded to the north, west, and south yielding a total of 71 stations. In 1988, another grid of 71 stations was sampled with slightly different spatial coverage. We used a small-scale version (0.25 m^2) of the BIONESS, a multiple opening and closing net, fitted with seven 333-μm-mesh nets. Seven discrete depths were sampled at each deployment and sample depths were spaced at 5-m intervals starting at 5 m (below surface). Each depth stratum was sampled for 10 min during which approximately 200 m^3 of water was filtered. Sensors positioned on the net frame provided real-time on–deck readouts of pitch, roll, and flow rate, as well as temperature, salinity, and depth (CTD). During the middle of each BIONESS tow, a horizontal tow of 10 min duration was made at 1 m depth with a 333-μm, 0.75-m diameter net.

All samples were preserved in 4% formalin buffered with sodium borate. All fish larvae and macrozooplankton were sorted from the samples and counted. Total length measurements were made using an ocular micrometer for larvae <15 mm and a millimetre scale ruler for larger larvae (≥ 15 mm) and juveniles.

Variations in the depth distributions of larvae and juveniles of the three species were evaluated by calculating the vertical centre of mass of their distributions, z_{cm}:

$$(1)\quad z_{cm} = \sum_j (p_j z_j),\ j = 1, m$$

where p_j is the proportion of larvae in the jth depth interval, z_j is its average depth, and m is the number of intervals. The centroids of the horizontal distribution of vertically averaged larval density were computed from

$$(2)\quad x_{cm} = \frac{\sum_k N_k x_k}{\sum_k N_k}, \qquad y_{cm} = \frac{\sum_k N_k y_k}{\sum_k N_k}, \qquad k = 1, n$$

where N_k is the larval density, x_k and y_k are the horizontal coordinates of the kth station, and n is the number of stations.

Inferred Spawning Areas

For an egg or larva released at horizontal position $\mathbf{X}_i$ at time t_i, its position at some later time t_f is

$$(3)\quad \mathbf{X}_f = \mathbf{X}_i + \int_{t_i}^{t_f} \mathbf{U}_L(\mathbf{X}_i, t)\, dt$$

where $\mathbf{U}_L(\mathbf{X}_i, t)$ is its Lagrangian velocity (relative to the seafloor) at time t. This velocity includes both the motion of the egg/larva relative to the water and the space- and time–dependent water velocity. To evaluate the influence of physical advection on larval distributions, we assumed that the individual larvae move with the ambient water and approximated this velocity by the velocity $\mathbf{u}_m(\mathbf{x}_m, t)$ observed at a current meter position $\mathbf{x}_m$. Taking t_f to be the midtime of the September survey, the mean release time can be approximated by

$$(4)\quad t_i = t_f - (l_f - l_i)/g$$

where l_f is the larval length from the September survey, l_i the length at release, and g its average growth rate. Thus, the release position can be estimated from

$$(5)\quad X_i = X_f - \int_{t_i}^{t_f} u_m(x_m, t)\, dt$$

with X_f, t_f, and l_f specified from the September survey data, $u_m(t)$ from the moored current measurements, and l_i and g from literature values. The use of current observations from a single position assumes that there is limited horizontal structure in the subtidal currents which dominate long term drift on the Southeast Shoal. Cross-spectral analysis of the 1987 moored observations indicates that the spatial scale of the subtidal currents over the Shoal is of the order 50–100 km, although around the Shoal's perimeter, there is substantial structure associated with the Labrador Current and the steep bathymetry. Hence, the accuracy of X_i estimated from (5) will generally decrease for earlier release times (older larvae) if positions are considerable distances from the mooring site.

In the analysis presented here, the length at release was taken as the hatching length and the growth rate chosen to be appropriate to post-hatching. Strictly speaking, the inferred release times and positions are therefore appropriate to hatching. However, because the egg phase is short relative to the larval drift time, they also approximate the spawning times and positions.

Results

Physical Oceanography

The temperature distributions observed along 44°15′N during the September survey in each year (Fig. 2) indicate a pronounced vertical stratification with a sharp thermocline near 20 m, consistent with historical observations (Loder 1991). Some interannual variability is apparent, including cooler temperatures and a less pronounced thermocline in 1986, and warmer near-surface waters and a slightly deeper thermocline in 1988. The vertical sections also show elevated near-bottom temperatures in the vicinity of the Shoal in each year, again consistent with historical observations (Loder 1991), and subzero temperatures along the Bank's eastern edge consistent with the presence of the cold intermediate layer associated with the Labrador Current (Petrie et al. 1988). Areal distributions of bottom temperature (Fig. 3) during early spring, early summer, and late summer (from the MEDS and hydrographic survey data) confirm the persistence of these features during spring and summer of each year, although with some variability in spatial structure and temperature from year to year (also see Carscadden et al. 1989).

The current measurements derived from the moored instruments revealed that, although the subtidal currents are important to long-term drift on the southern Grand Bank (Loder et al. 1988), they are generally weak. The mean currents have magnitudes of up to 0.04 m/s, while the standard deviations of the low-frequency current components are typically 0.02–0.05 m/s (Ross et al. 1988). The expected particle drifts resulting from the measured currents are illustrated in Fig. 4 which presents progressive vector plots for the central and eastern sites (Fig. 1) in 1987. Typical of the central and western sites in the other years, the central-site drift is generally westward and significantly stronger at the upper meter. In

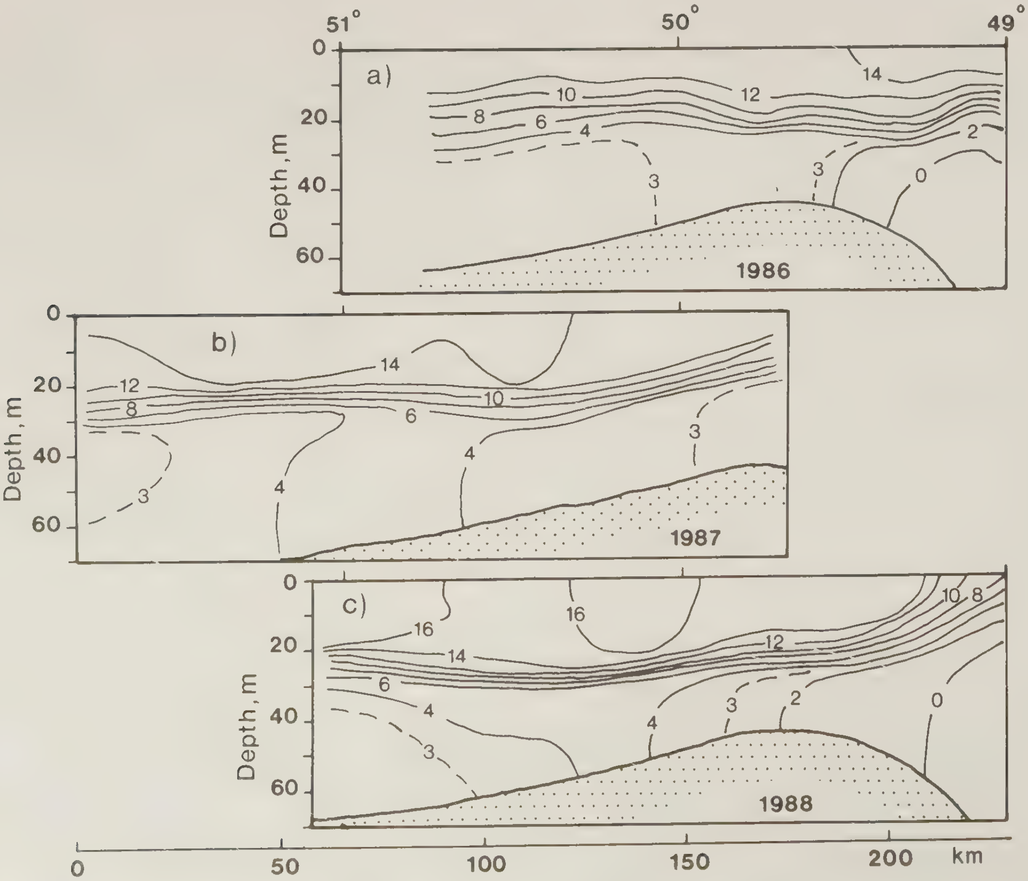


FIG. 2. West–east vertical sections of temperature along 44°15′N from the CTD mounted on the BIONESS during the September larval surveys of (a) 1986, (b) 1987, and (c) 1988.

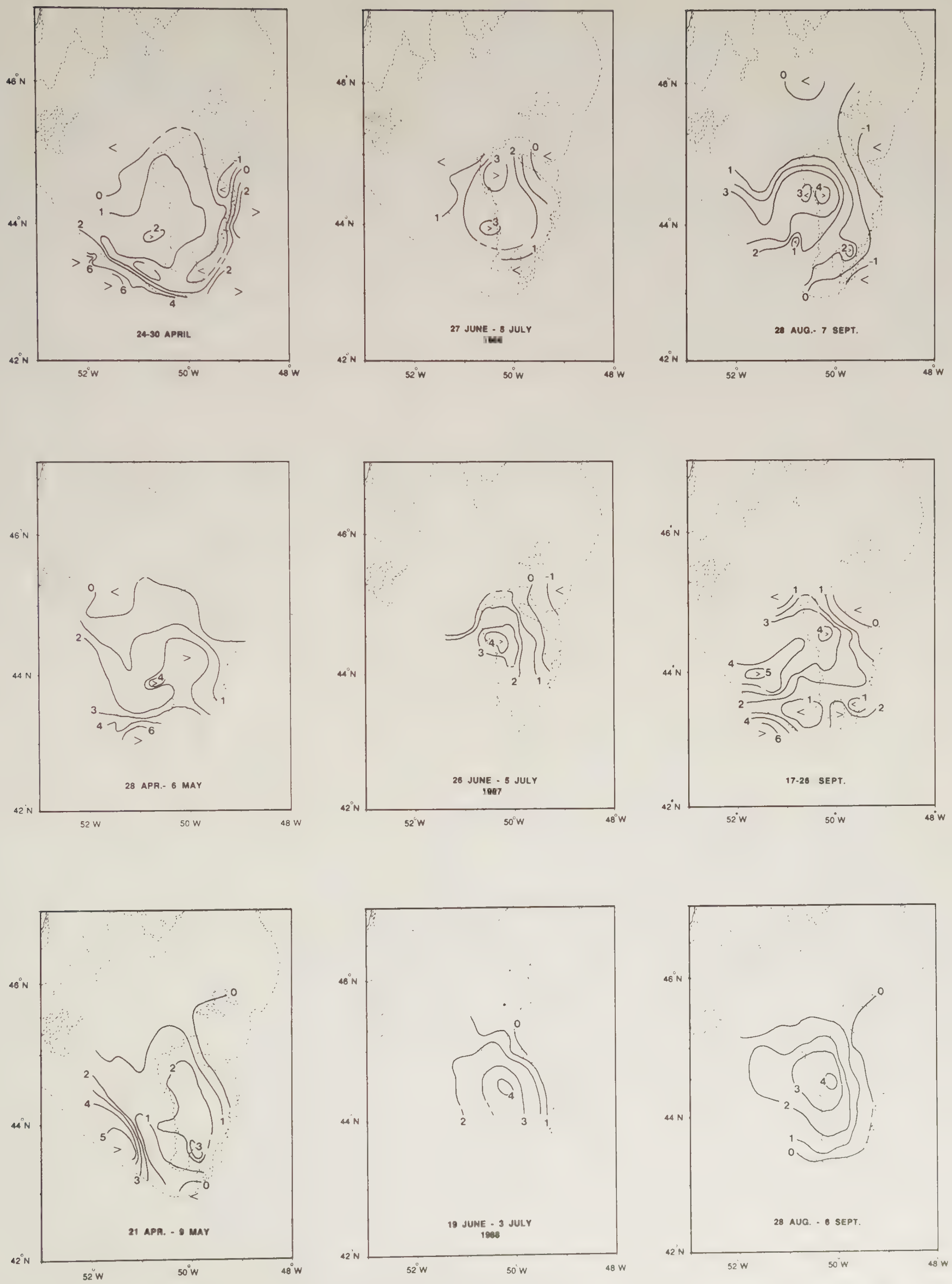

24-30 APRIL
27 JUNE - 8 JULY
28 AUG.- 7 SEPT.
28 APR.- 6 MAY
26 JUNE - 5 JULY
1987
17-26 SEPT.
21 APR. - 9 MAY
19 JUNE - 3 JULY
1988
28 AUG. - 8 SEPT.
46°N
44°N
42°N
52°W
50°W
48°W

FIG. 3. Bottom temperature distributions on the southern Grand Bank during early spring, early summer, and late summer in 1986, 1987, and 1988. Data are from dedicated hydrographic surveys and MEDS and have been sorted into time intervals with broad spatial coverage.

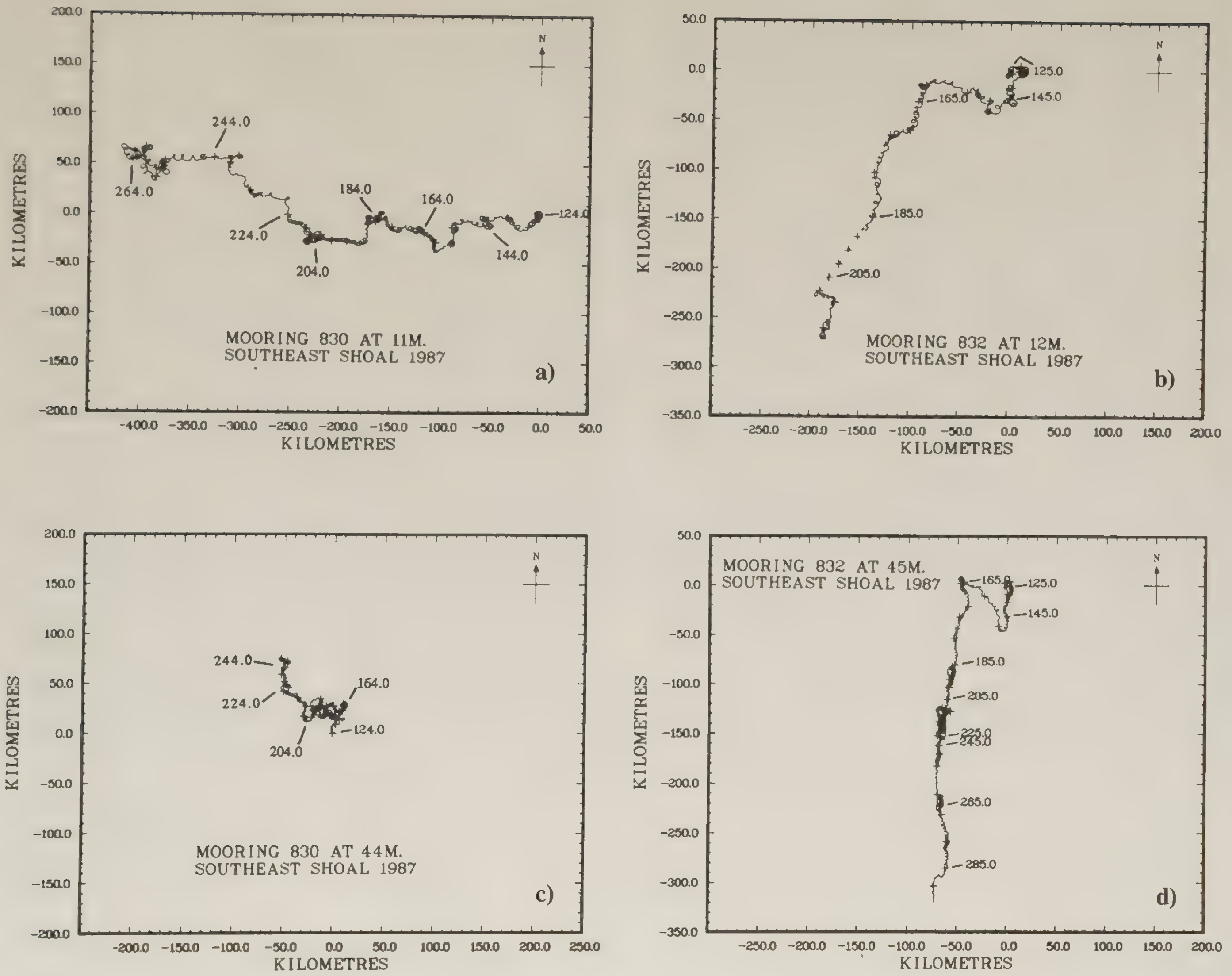


FIG. 4. Progressive vector plots from current meters at the (a, c) central (mooring 830) and (b, d) eastern (mooring 832) sites in 1987. Crosses denote 5-d intervals, labelled every 20 or 40 d.

contrast, the eastern-site drift is generally southward. These drifts are consistent with barotropic numerical model predictions (Greenberg and Petrie 1988; Hukuda et al. 1989) of a strong southward Labrador Current along the Bank's eastern edge and a weak west to northwestward drift across the Bank. The mean currents (Fig. 5) confirm the interannual persistence and large space scales of the characteristic drifts, but also indicate quantitative variations.

The moored measurements at the central site also revealed a large decrease in temperature over much of the water column in August 1986. This was associated with both vertical mixing and the displacement of Labrador Current water onto the Shoal during the passage of a tropical storm (Loder and Ross 1988; Frank and Carscadden 1989) and contributed to the relatively cool 1986 September temperatures (Fig. 2).

Adults

Commercial abundances of American plaice, yellowtail flounder, and witch flounder are common on the Grand Bank. As a result, their seasonal distributions and those of prespawners are documented. Of the three, yellowtail inhabits the shallowest and warmest portions of the Bank. In fact, in this area, yellowtail is at the northern limit of its commercial range. As a result, temperature appears to be an important regulator of its distribution. In the early 1960's yellowtail abundance on the Bank increased coincident with a decrease in haddock abundance and an upward trend in bottom temperature (Pitt 1970). During the 1950's and 1960's, the greatest concentrations of yellowtail occurred at depths of 57–64 m, coincident with bottom temperatures of 3.1–4.8°C (Pitt 1970). Research trawl surveys conducted during the 1970's and 1980's revealed the largest concentration of yellowtail to be at depths less than 100 m where water temperatures exceeded 1°C (Wells et al. 1988). Fitzpatrick and Miller (1979) used research trawl data to delimit the distribution (Fig. 6) of ripe fish between 1952 and 1968. During this interval, peak spawning occurred during the latter half of June in areas where bottom temperatures exceeded 2°C (Pitt 1970). Since the warmest summertime bottom temperatures on the Grand Bank occur over the Southeast Shoal (Loder 1991; Fig. 3), the Shoal is probably the most important spawning area for yellowtail on the Bank.

In contrast with yellowtail, plaice occurs in deeper waters and is considered a cold-water species. It is reported to occur

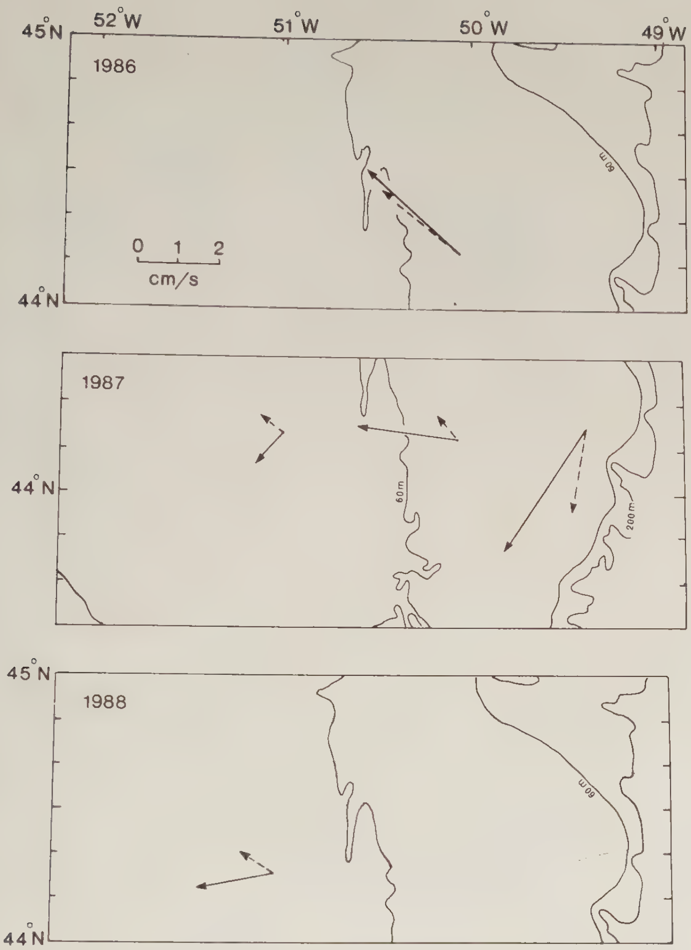


FIG. 5. Record-mean currents from moored measurements on the southern Grand Bank in 1986–88. Solid vectors are for upper instruments; broken vectors are for lower meters.

at depths ranging from 90 to 250 m and at temperatures from just below 0 to 1.5°C (Scott and Scott 1988; Wells et al. 1988). Plaice appears to spawn in most areas where the influence of the cold Labrador Current is apparent (Fig. 6). There is, however, some dispute concerning the relative importance of different areas. Pitt (1966) reported that the northern and eastern slopes of the Bank supported the greatest spawning activity. Nevinsky and Serebryakov (1973) also noted the importance of the northern Grand Bank but reported that spawning on the eastern, southwestern, and southern slopes was less intense. They concluded that spawning occurs from April to mid-May at bottom temperatures ranging from −1.3 to 3.5°C, with spawning being most intense at 0–2°C. Pitt (1966) reported that average spawning temperatures ranged from −1.3 to 2.8°C on the northern, southeastern, and southwestern areas of the Bank.

Witch is generally considered to be a deepwater species, residing in gullies where the bottom is clay and mud rather than on sand and gravel bottom typical of the banks and the inshore (McKenzie 1955). In the Grand Bank area, research trawl surveys conducted during 1958–74 have revealed that the greatest numbers of witch occurred at depths of 185–366 m and at bottom temperatures of 2–6° (Bowering 1976). On the basis of the relative frequencies of ripening and recently spent fish from research surveys, Bowering (1990a) concluded that spawning occurs during April–June (Fig. 6) on the southern Grand Bank at depths ranging between 100 and 200 m and temperatures between 2 and 3°C.

None of the three flatfish species discussed is reported to undergo extensive migrations, although yellowtail and plaice migrate seasonally, moving into shallow water in the spring and into deeper water during the winter (Scott and Scott 1988; Walsh 1991).

Larval Distributions and Size Composition

Yellowtail flounder

The depth of the centre of mass of yellowtail larvae and juveniles occurred at 24.2, 28.0, and 26.7 m during the day and 18.6, 23.9, and 25.1 m during the night in 1986, 1987, and 1988, respectively (Fig. 7). This diel pattern of depth distribution is similar to that described by Smith et al. (1978), but the day–night change in depth in the mid-Atlantic Bight was greater, exceeding 25 m. In view of the limited day–night change observed on the southern Grand Bank, we combined the centre of mass depths for day and night when estimating the direction and magnitude of larval drift (Table 2).

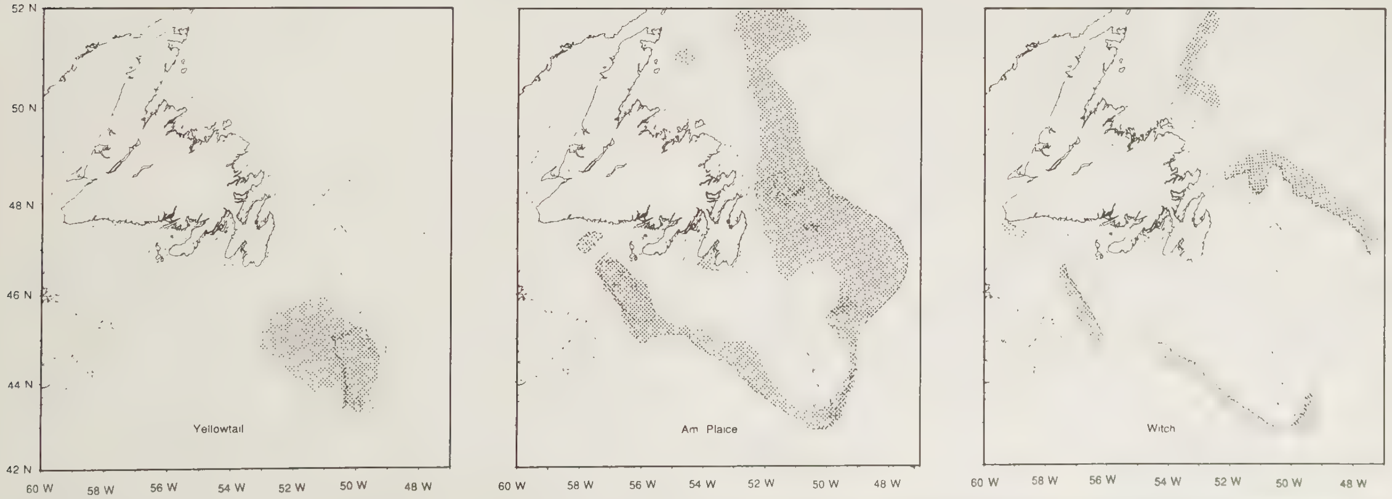


FIG. 6. Composite picture of spawning distributions of yellowtail and plaice (after Fitzpatrick and Miller 1979) and witch (after Bowering 1990a) in the Grand Banks region for April–July.

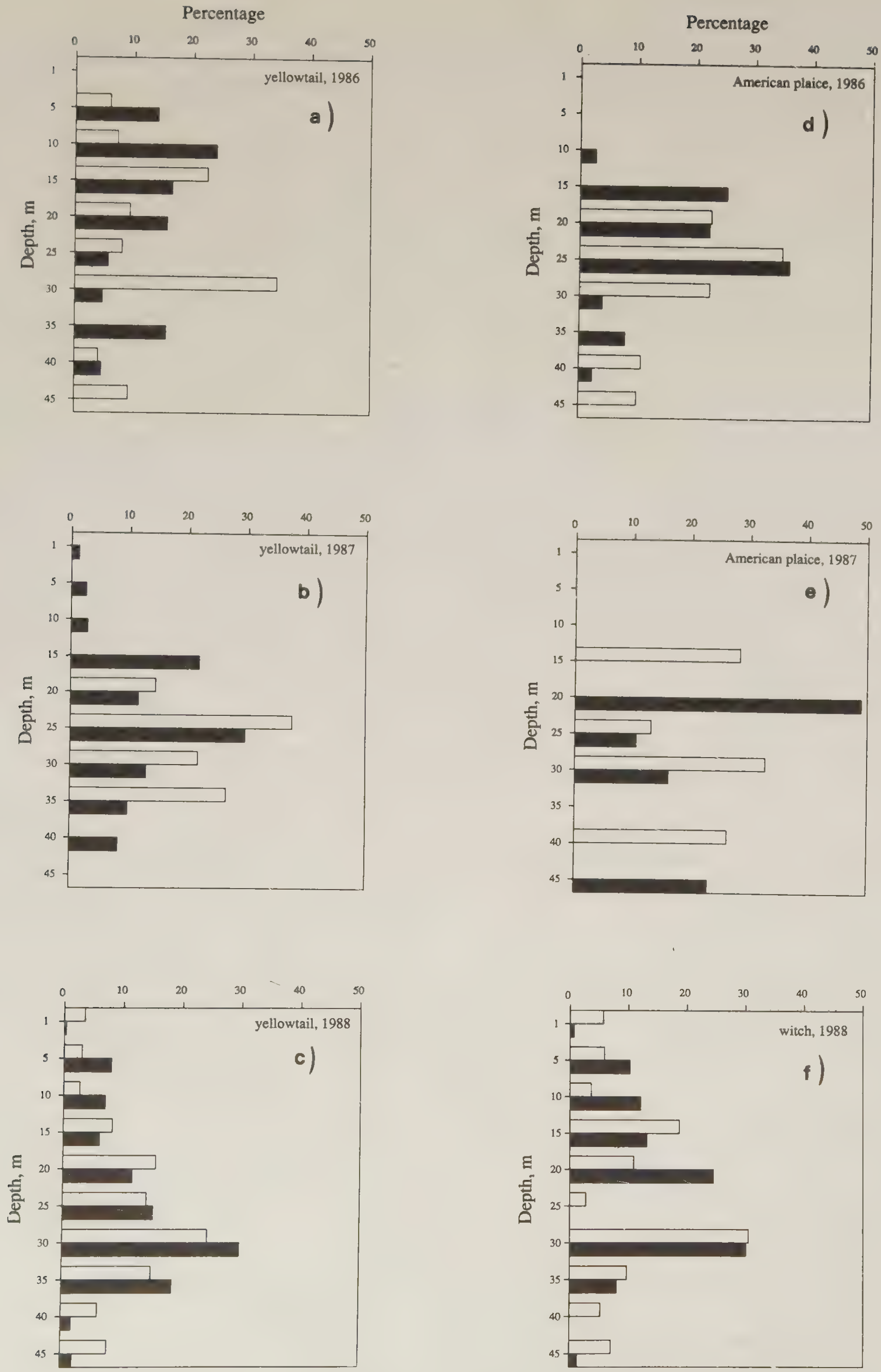


FIG. 7. Percentage of larvae in various depth intervals for yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988. Distributions are shown for both day (open bars) and night (shaded bars) stations.

Furthermore, peak concentrations of yellowtail were observed at depths near or below the thermocline (Fig. 8). In 1986 and 1987, a majority of the yellowtail (>60%) were below the thermocline. Given the two-layer stratification, bottom temperature was taken as an index of the (lower-layer) thermal regime principally experienced by the larvae and juveniles.

In 1986 the highest concentrations of yellowtail occurred over the western half of the survey area where bottom temperature generally exceeded 2°C (Fig. 9a, 9g, 10a). No yellowtail were

TABLE 2. Summary of midtimes (t_f) of surveys, observed mean vertical positions (z_{cm}) and larval lengths (l_f), assumed hatching lengths (l_i) and growth rates (g), and calculated ages (post-hatching) and spawning dates (t_i) for the larval cohorts observed in September of each year.

Cohort	t_f (d)	z_{cm} (m)	l_f (mm)	l_i (mm)	g (mm/d)	Age (d)	t_i (d)
Yellowtail							
1986	258	23.2	23.1	3.5	0.11	178	80
					0.25	78	180
1987	264	24.7	26.0	3.5	0.11	205	59
					0.25	90	174
1988	264	25.7	18.7	3.5	0.11	138	126
					0.25	61	203
Plaice							
1986	258	24.3	27.8	4.0	0.16	149	109
					0.25	95	163
1987	264	29.1	30.1	4.0	0.16	163	101
					0.25	104	160
Witch							
1988	264	22.8	18.3	4.5	0.09	153	111
					0.25	55	209

found on the eastern portion of the Bank where temperature was generally less than 2°C. The highest yellowtail concentrations occurred west of the peak temperatures, but the westward limits of the distribution were not resolved.

The 1987 yellowtail distribution (Fig. 9b) exhibited some similarity with that of 1986, although the average density was substantially lower. Maximum densities occurred on the northwestern portion of the Shoal. Very few individuals were collected in the eastern, southern, or southeastern sections of the grid. As in 1986, the highest catches were generally obtained at stations where bottom temperature (Fig. 9h, 10b) exceeded 2°C. However, the yellowtail and temperature maxima were again offset, with peak yellowtail densities to the north of the temperature peak. The northwestward limit of the yellowtail distribution was not resolved.

The average density of yellowtail in 1988 (Fig. 9c) was similar to that observed in 1986. Peak abundances were again coincident with bottom temperatures above 2°C (Fig. 9i, 10c), with densities declining from west to east. Unlike 1986 and 1987, the extent of the yellowtail patch was better defined and the patch coincided with the temperature maximum. There was also bimodality in the yellowtail–temperature relation, with highest densities occurring at temperatures between 0 and 1°C and above 2°C (Fig. 10c). The observations from all three years support a relation between the horizontal distributions of yellowtail and lower-layer temperature, although it is unclear whether or not there is a direct influence.

The lengths (l_f) of yellowtail collected in September 1986 ranged from 10 to 33 mm with a mean of 23 mm (Fig. 11a; Table 2). Literature values for larval growth rate (g) range from an average of 0.11 mm/d for larvae collected over the Grand Bank during June–August 1980 (Bonnyman 1983) to 0.25 mm/d for larvae reared in the laboratory at 10°C (Smigielski 1979). Hatching length (l_i) is approximately 3.5 mm (Fahay 1983). Assuming that the growth rates were similar in all areas, as well as before and after metamorphosis, we estimate from (4) that the mean age (post-hatch) of yellowtail captured in 1986 was in the range of 78–178 d (Table 2). In September 1987, the mean length of yellowtail was 26 mm (Table 2), with most individuals lying between 22 and 34 mm (Fig. 11b), although individuals as small as 5 mm were captured. In September 1988, yellowtail sizes ranged from 4 to 33 mm (Fig. 11c), with a mean of 19 mm (Table 2). For the above growth rates and hatching length, the mean ages of larvae sampled in 1987 and 1988 were in the ranges of 90–205 and 61–138 d, respectively (Table 2). While the uncertainty in the growth rate results in a wide mean age range, the historical data on spawning times (e.g. Fitzpatrick and Miller 1979) suggest that the lower ages are more probable. The wide range of sizes (and ages) coincident in time and space in each of the three years also suggests that there is some retention of the early life stages (larvae and pelagic juveniles) of yellowtail on the Southeast Shoal.

American plaice

There was little evidence of vertical migration by plaice larvae and juveniles in the 1986–88 observations. The average centres of mass for day and night generally occurred at depths exceeding 20 m (Fig. 7d, 7e). Since there are no other published data on the depth distribution of the early stages of plaice, we used the mean depth for the day and night observations combined to estimate drift (Table 2). Peak plaice concentrations were located near the thermocline, with greater than 70% of the larvae and juveniles below the thermocline in 1986 and 1987 (Fig. 8d, 8e). As with yellowtail, bottom temperature was used as an index of the lower-layer thermal regime in our evaluation of the horizontal distributions of plaice.

The horizontal distribution of plaice in September 1986 was inversely related to that of yellowtail (Fig. 9a, 9d). Plaice densities increased from west to east across the Shoal and peaked along its eastern flank where bottom temperatures were below 1°C (Fig. 9g, 10d). Only a few plaice were found in the western and central parts of the grid where temperatures exceeded 2°C (Fig. 9d, 9g).

The 1987 and 1988 plaice densities were approximately two orders of magnitude lower than those from 1986. However, the distributions were similar in all three years. In each of 1987 (Fig. 9e) and 1988 (not shown), plaice were captured at only 8 of 71 stations. These were located primarily along the eastern half of the grid where bottom temperatures were near or below 0°C. There were also some occurrences of plaice at stations with higher temperatures (Fig. 9e, 9h, 10e).

The ranges in length of plaice collected during the September surveys were 16–38 mm (Fig. 11d), 25–35 mm (Fig. 11e), and 10–38 mm (not shown) for 1986, 1987, and 1988, respectively. The mean lengths in 1986 and 1987 were 28 and 30 mm (Table 2). Growth rates of plaice larvae on the Grand Banks average 0.16 mm/d during May–September (Bonnyman 1983), while rates average 0.25 mm/d over the first 80 d in the Wadden Sea (Zijlstra et al. 1982). For these growth rates and a hatching length of 4.0 mm (Fahay 1983), the mean age of the 1986 and 1987 plaice cohorts was estimated to be in the ranges of 95–149 and 104–163 d, respectively (Table 2). Given the limited occurrence of plaice over the Southeast Shoal, we suggest that their distribution is primarily influenced by Labrador Current advection along the Bank edge to the northeast of the study region. The occurrence of plaice on the eastern Shoal may result from leakage of the Current onto the Bank followed by a weak westward drift.

Witch flounder

The depth of the centre of mass of witch larvae and juveniles in 1988 was 21 m at night, 26 m during the day, and 23 m for both combined (Fig. 7f; Table 2). Peak concentrations were in the thermocline (Fig. 8f). However, the larvae were broadly

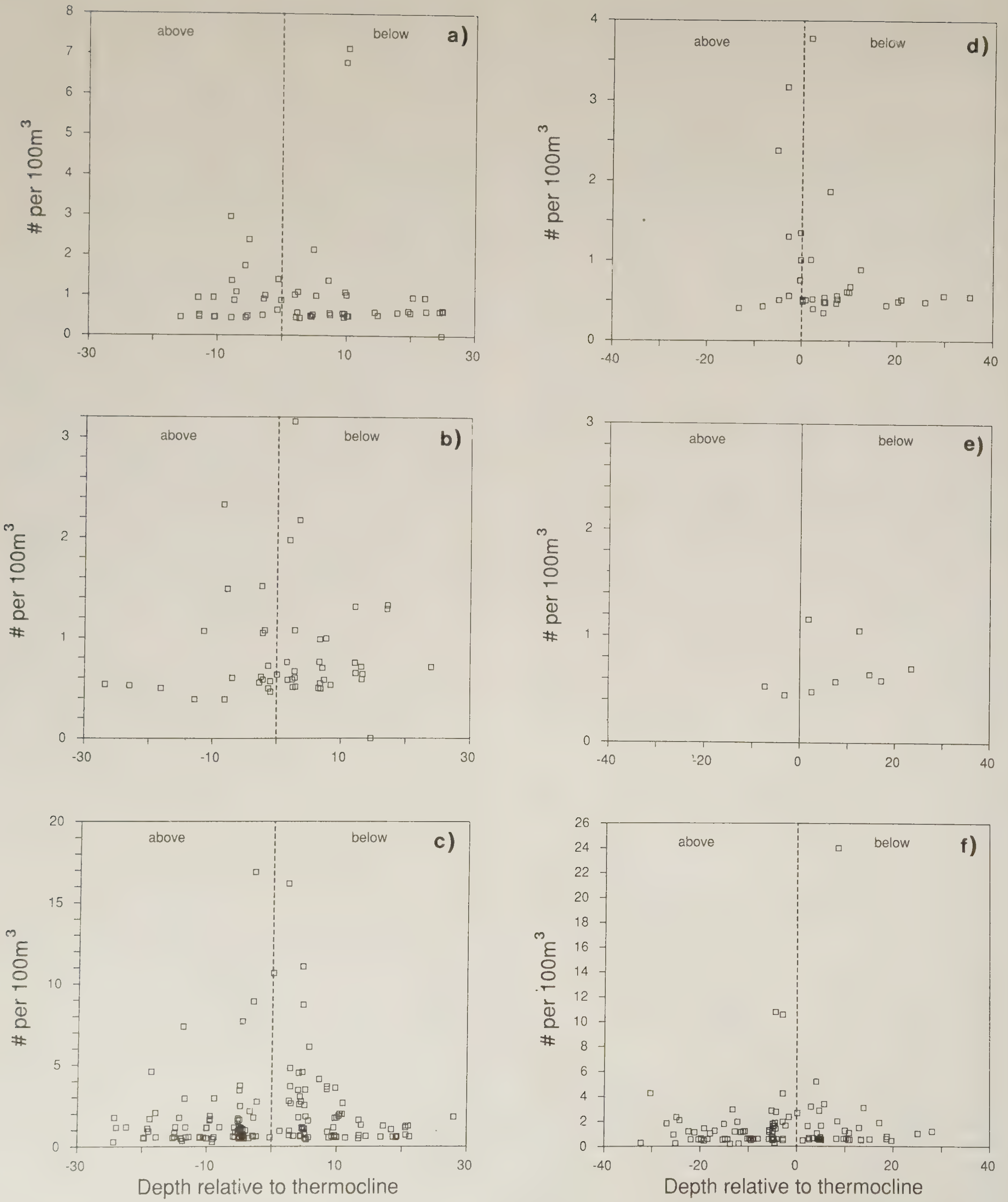


FIG. 8. Scatter plots of larval density versus depth (m) relative to the thermocline for yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988.

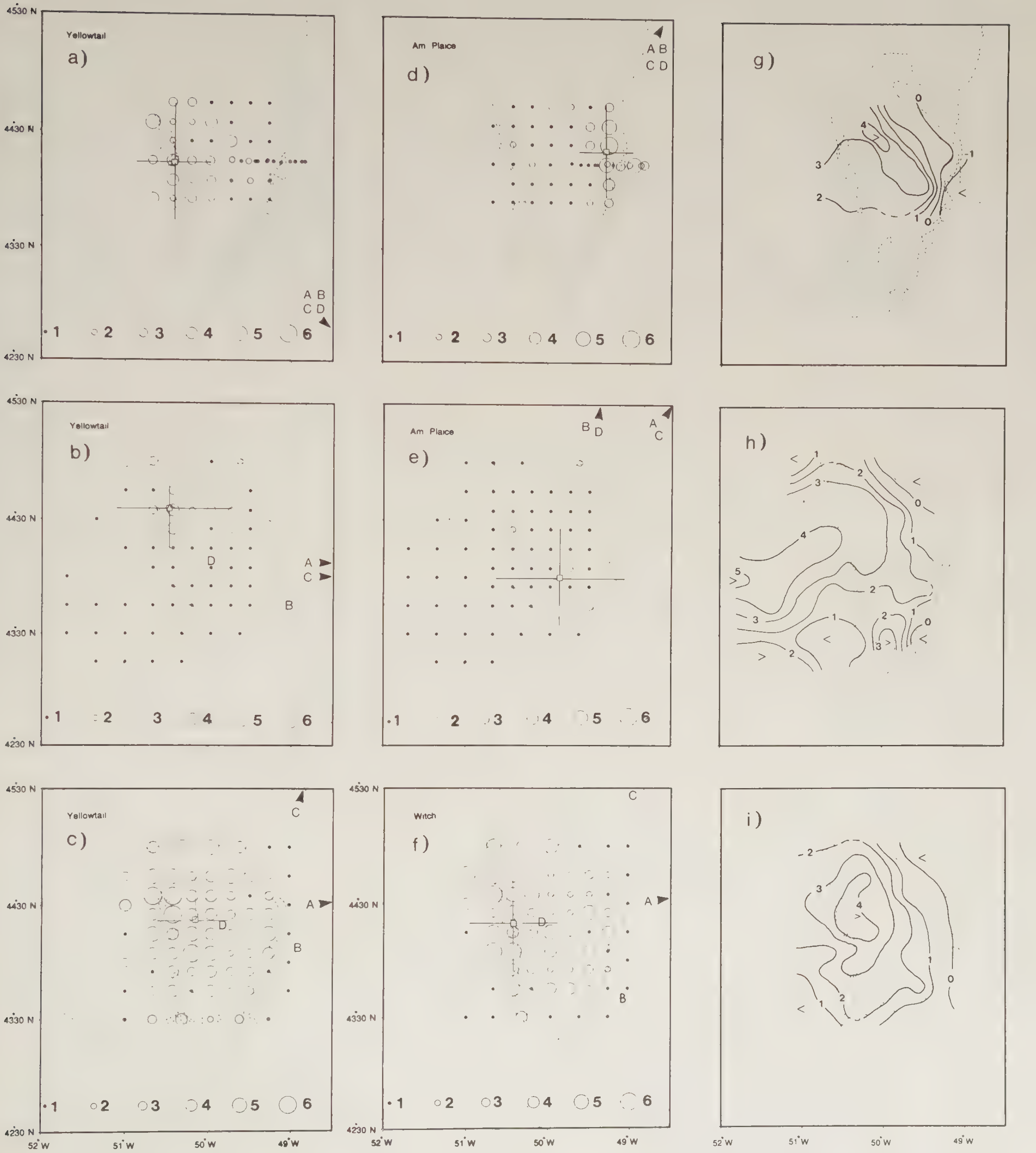

4530 N
4430 N
4330 N
4230 N
52°W
51°W
50°W
49°W
Yellowtail
a)
A B
C D
•1 ∘2 ◌3 ◯4 ◯5 ◯6
Am Plaice
d)
A B
C D
•1 ∘2 ◌3 ◯4 ◯5 ◯6
g)
0
1
2
3
4
Yellowtail
b)
D
A
C
B
•1 2 3 4 5 6
Am Plaice
e)
B D
A C
•1 2 3 4 5 6
h)
0
1
2
3
4
5
Yellowtail
c)
C
A
D
B
•1 ∘2 ◌3 ◯4 ◯5 ◯6
Witch
f)
C
A
D
B
•1 ∘2 ◌3 ◯4 ◯5 ◯6
i)
0
1
2
3
4

FIG. 9. Distributions of depth-averaged larval density and bottom temperature (g, h, i) from surveys during (a, d, g) 13–18 September 1986 (days 256–261), (b, e, h) 17–26 September 1987 (days 260–269), and (c, f, i) 17–23 September 1988 (days 261–267). Larval distributions are shown for yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988. Keys to the expanding symbols: (a, b, c) 1: none, 2: 0.05–0.13, 3: 0.13–0.31, 4: 0.31–0.78, 5: 078–2.0, and 6: >2.0; (d, e, f) 1: none, 2: 0.05–0.1, 3: 0.1–0.2, 4: 0.2–0.4, 5: 0.4–0.8, and 6: >0.8,where all densities are numbers per 100 m^3. Centroid positions and second moments of the larval distributions are also shown. The capital letters (A, B, C, D) indicate the inferred spawning locations presented in Table 3.

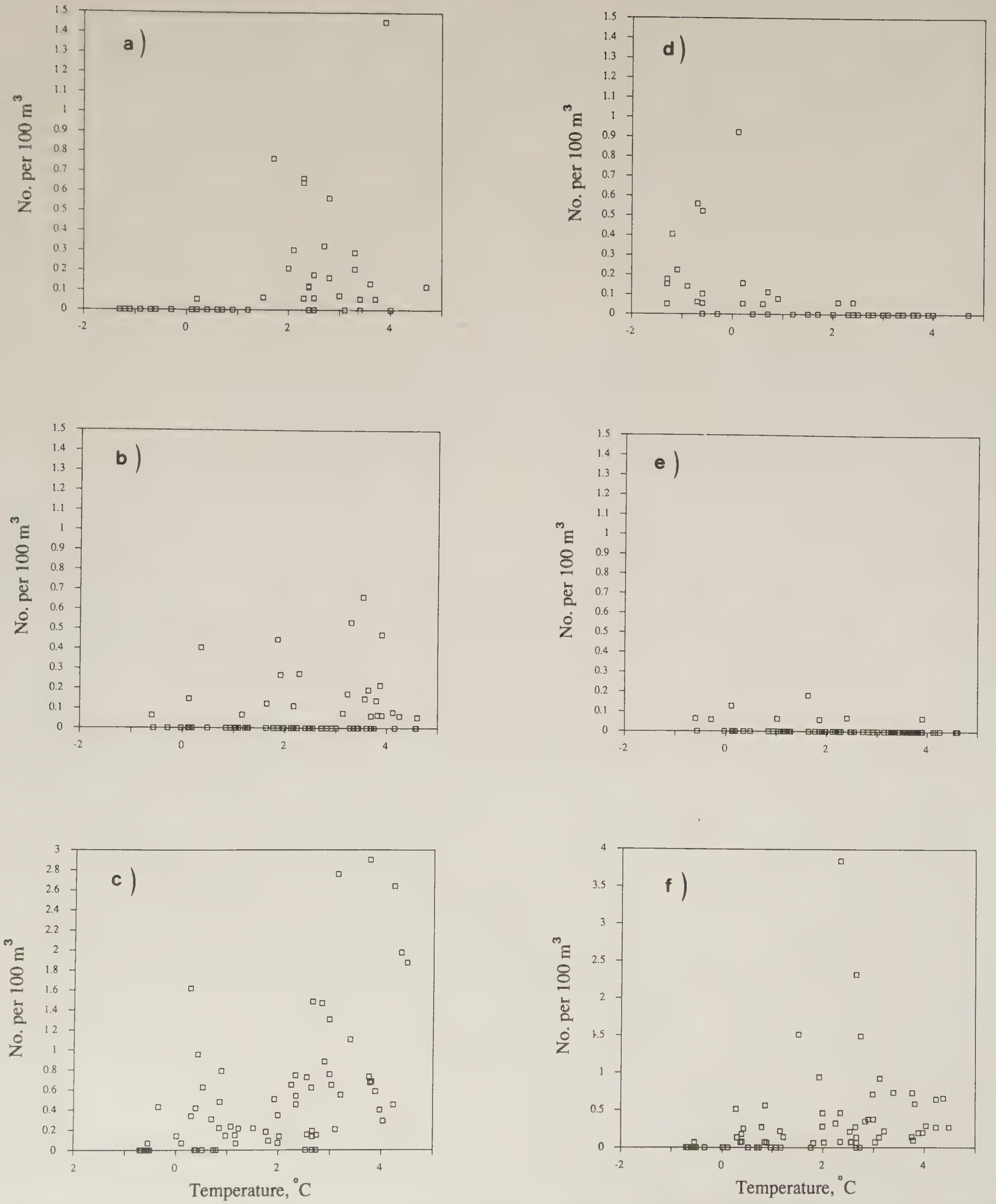


FIG. 10. Scatterplots of larval abundance versus bottom temperature for yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988.

distributed over the water column, with roughly equal proportions occurring above and below the thermocline. As with the other species, we used bottom temperature as an index of the lower-layer thermal regime in examining the horizontal distribution of witch.

Witch occurred as single individuals at only 2 of 47 stations in September 1986 and 3 of 71 stations in 1987. They were abundant during the 1988 survey (Fig. 9f) when their average density equalled that of yellowtail. In 1988, witch larvae and pelagic juveniles were most abundant over the central, western,

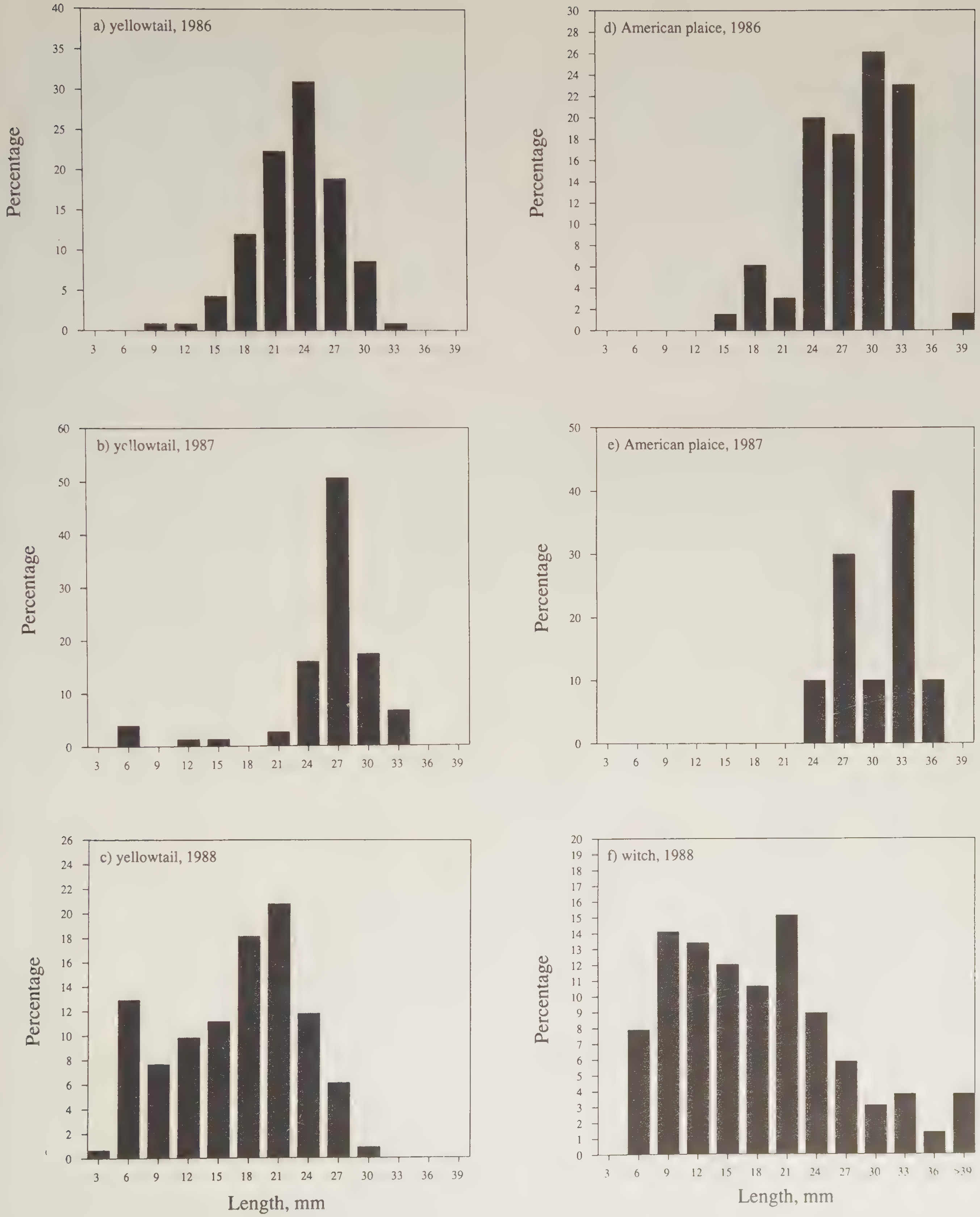


FIG. 11. Length frequency distributions of yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988.

and northwestern portions of the survey area, particularly where bottom temperatures exceeded 2°C (Fig. 9f, 9i, 10f). They were absent from the eastern edge of the survey where temperatures were near 0°C. The witch distributions were thus similar to those of yellowtail, with maximum densities occurring in relatively warm bottom waters (Fig. 9).

The length of witch collected in 1988 ranged from 5 to 50 mm, with a mean of 19 mm (Fig. 11f). The only published estimate of growth rate for witch (0.09 mm/d) is based on monthly collections from the southern Grand Bank (Bonnyman 1983). We assumed an upper limit growth rate of 0.25 mm/d consistent with that of the other two species. Given a hatching length of 4.5 mm and the above growth rates, we estimated a mean age for witch in our samples ranging from 55 to 153 d (Table 2).

Inferred Spawning Positions

To examine whether the larval distributions and the estimated ages at capture are consistent with passive advection from sites with historical distributions of prespawning fishes, we used (5) to estimate the spawning (hatching) sites by species and year for a range of input values. Examination of (4) and (5) indicates that there will be uncertainty in the inferred sites associated with uncertainties in l_f, l_i, g, $\boldsymbol{X}_f$, and the horizontal and vertical structure of $\boldsymbol{u}_m$ (taking passive advection as a given). However, consideration of the available information suggests that the largest contributors to this uncertainty are the growth rates, the depth of the larvae during the drift period, and horizontal structure in the currents near the Bank edge. To provide approximate bounds on the likely sites, we show in Table 3 the expected larval displacements ($\boldsymbol{X}_f - \boldsymbol{X}_i$) for four cases (A, B, C, D) for each species and year. These are estimates based on the two different mean ages (or spawning dates) shown in Table 2 and estimates for currents typical of the upper (A, C) and lower (B, D) water columns (current meters). For yellowtail and witch, current measurements from the respective years are used, while the 1987 measurements from the eastern mooring site are used for plaice in both 1986 and 1987. The estimated spawning positions for the different cases are indicated in Fig. 9.

For most of the cases considered, the inferred spawning positions are off the Bank in areas which are represented poorly by the moored measurements. The specific positions in those cases have limited meaning, but the prediction of remote spawning sites under the assumed conditions should nevertheless be valid. In particular, the moored measurements of upper-layer currents strongly suggest that, if larvae occupy these surface waters through the summer and are transported passively, spawning must occur well away from the Southeast Shoal (cases A, C). In contrast, passive advection by lower-layer currents does allow for spawning sites in the vicinity of the Shoal, particularly if growth rates approximate 0.25 mm/d (case D).

TABLE 3. Estimated displacements of spawning positions (x_i, y_i) from September observation positions (x_f, y_f) for various species and years. Results are shown for four cases for each species/year: two different spawning dates (growth rates) taken from Table 2 and drifts as measured at the upper (cases A, C) and lower (cases B, D) current meters. A positive x-displacement denotes a spawning site to the east of the September larval position, and a positive y-displacement denotes a spawning position to the north of the September position. Where current measurements are available for the entire drift period, they are used; otherwise the record-mean currents are used. See Fig. 9 for estimated spawning positions.

Cohort	Case	Spawning date (d)	Drift depth (m)	$x_i - x_f$ (km)	$y_i - y_f$ (km)	Current source: period and mooring No.
Yellowtail						
1986	A	80	20	370	−370	Record mean @ 774
	B		45	290	−290	
	C	180	20	160	−160	
	D		45	170	−190	Days 180–258 @ 774
1987	A	59	11	490	−53	Record mean @ 830
	B		44	120	−90	
	C	174	11	280	−70	Days 174–264 @ 830
	D		44	39	−54	Record mean @ 830
1988	A	126	13	250	33	Days 126–262 @ 887
	B		63	94	−58	
	C	203	13	110	130	Days 203–262 @ 887
	D		63	21	4	
Plaice						
1986	A	109	12	280	420	Record mean @ 832
	B		45	64	280	
	C	163	12	180	270	
	D		45	41	180	
1987	A	101	12	310	460	
	B		45	70	310	
	C	160	12	200	290	
	D		45	25	230	Days 160–264 @ 832
Witch						
1988	A	111	13	280	40	Record mean @ 887
	B		63	110	−70	
	C	209	13	110	130	Days 209–262 @ 887
	D		63	28	2	

Yellowtail flounder

For yellowtail, the observed 1987 and 1988 larval distributions are consistent with spawning over the Shoal if larvae drift with the lower-level currents and experience a high growth rate (case D) (Fig. 9b, 9c). The bottom temperature distributions (Fig. 3) during the late June/early July spawning times inferred for the high growth rate for 1987 and 1988 show values above 2°C in the vicinity of the inferred spawning sites. Although the measured (northwestward) lower-level currents in 1986 were stronger than in 1987 and 1988 (Fig. 5) and imply an off-bank spawning site, the bottom temperature (and salinity, not shown) distributions (Fig. 3) suggest persistence of relatively warm bottom water over the Shoal during spring–summer and an intrusion of water from the west. Given the suggested increased spatial structure of the near-bottom currents in 1986, the possibility that lower-layer residence times were greater than that implied by the current measurements cannot be discounted. For the other cases (A, B, C), the inferred yellowtail spawning sites were off the Bank, although the sites for lower-level drift and slow growth in 1987 and 1988 were close to the Shoal.

American plaice

Given that the September plaice distributions were concentrated along the eastern edge of the Bank where the measured currents were southward, the inferred spawning positions are well to the north of the study area. Only the slower growth rate yielded spawning times (Table 2) consistent with historical information. The inferred spawning positions under these conditions are in the vicinity of historical spawning sites on the northern–northeastern Grand Bank (Fig. 6), but it is not possible to discriminate between upper- and lower-layer drift. However, passive advection in the core of the Labrador Current where the residual current speeds are substantially greater than those observed at the eastern mooring site (Mountain 1980; Greenberg and Petrie 1988) would not lead to the distribution observed. The bottom temperatures on the eastern Bank in the study years (Fig. 3) are consistent with a cold intermediate layer, with temperatures in the range observed historically for plaice spawning.

Witch flounder

Given the low densities of witch observed in 1986 and 1987, we estimated spawning sites for 1988 only. In that year the range of expected growth rates generates spawning times that are consistent with historical observations and, assuming drift with the lower-level currents, implies spawning positions (Fig. 9f) which bracket the historical sites. In contrast, drift in the upper-level currents would require spawning positions well off the Bank. There are, however, some unresolved questions regarding the witch distributions (in addition to their occurrence in 1988 but not 1986 and 1987). Lower-level passive drift and a high growth rate (*D*) are unlikely, since they imply a Shoal spawning site inconsistent with the historical information presented in Bowering (1990a). Lower-level drift requires a slower growth rate (similar to B) in order to have an off-bank spawning site. However, our limited information on currents and hydrography on the eastern side of the Bank in 1988 makes the expected spawning position and its consistency with the temperature range of witch unclear. Thus, a witch spawning site on the eastern side of the Bank together with passive lower-layer drift cannot be discounted for 1988, although there is no direct evidence for this.

Discussion

The horizontal distributions of larvae and juveniles of the three flatfish species show a striking correspondence to the bottom temperature distributions, suggesting a probable influence of the physical environment on the early life stages of flatfish on the southern Grand Bank. Correlation analyses between depth-averaged densities and temperature and salinity at various vertical levels generally yielded the highest (significant) correlations for bottom temperature. There are, however, several unresolved questions. In particular, the full extent of the flatfish and temperature features was not resolved by the survey grids, the flatfish and temperature maxima appear to be offset in some cases (yellowtail in 1986 and 1987), the flatfish distributions extend through the thermocline into the upper layer while the bottom temperaures are representative of depths below 25–30 m (Fig. 2), and the mechanism(s) underlying the correspondence is unclear. It is unclear whether there is a direct temperature influence on larval distributions or whether larval densities and temperature are indirectly related by some common correlate (e.g. different water masses). One possible scenario linking larval distributions directly to temperature is passive advection of the eggs and larvae in subthermocline waters followed by active seeking, by late-stage larvae and juveniles, of the adults' preferred bottom temperature.

The vertical distributions observed during the September larval surveys are of limited value in identifying the origin of the larvae–temperature relation. Plaice distributions were dominantly subthermocline, but yellowtail and witch were distributed over the range of sampled depths with centres of mass near the thermocline. It is possible that the dominant sampling above 40 m missed a significant number of older larvae and juveniles at depth and biased the centres of mass towards the surface. Some support for this comes from annual flatfish surveys conducted in September over the southern Grand Bank using bottom trawling gear which occasionally capture 0-group yellowtail and plaice as small as 2 cm standard length (S. J. Walsh, Department of Fisheries and Oceans, St. John's, Nfld., pers. comm.). On the other hand, the observed depth distributions, especially the high concentrations near the thermocline, may promote fast growth and high survival for those individuals occupying depths of maximum thermal gradients, as previously documented for fish larvae inhabiting oligotrophic lake systems (e.g. see Wurtsbaugh and Neverman 1988).

Comparison of spawning sites inferred from the observed distributions and measured currents with historical concentrations of mature fishes provides some support for the hypothesis of passive advection in some but not all cases, and then only with significant provisos. For two of the three years sampled (1987, 1988), the yellowtail distributions were consistent with passive advection from a Southeast Shoal spawning site provided that the survivors drift in the lower water column and the growth rate is near the maximum value considered (0.25 mm/d). The spawning times inferred from this growth rate approximate historical descriptions, and the bottom temperatures observed in the vicinity of the inferred spawning locations and times are consistent with reported temperature preferences of adult yellowtail. However, the 1986 inferred spawning site for yellowtail was implausible. This may have been due to increased spatial structure in the lower-layer drift. Observations of yellowtail egg and early-stage larval distributions in other years (May–June 1983 (J. Anderson, Department of Fisheries and Oceans, St. John's, Nfld., pers. comm.), July 1985) support their persistence over the Shoal in summer as well as their occurrence to the northwest.

The observed plaice distributions in all three years suggest spawning along the northern or northeastern Grand Bank followed by southward advection in the Labrador Current. For plaice the current data are not adequate to discriminate between upper- and lower-layer drift. The historical spawning times for plaice are consistent with the slower growth rate considered (0.16 mm/d), and the historical sites imply slow rates of larval drift in the bankward portion of the Labrador Current.

For witch, there was little evidence that the 1988 distribution on the Shoal was consistent with historical spawning sites, although the possibility that they resulted from passive lower-layer drift from the Bank's eastern edge and a relatively slow growth rate could not be discounted. Among the three species studied, witch has the longest pelagic phase (up to 1 yr) (Scott and Scott 1988), suggesting that slow growth is a reasonable approximation. Indeed, the cooccurrence of yellowtail (historical spawning on the Bank) and witch (historical spawning on the sides of the Bank) larvae on the Bank in 1988 requires either earlier spawning for witch (and subsequent drift through the yellowtail spawning area) or dominant behavioural influences for one of the species.

While most of the above evidence in support of the passive advection scenario is inadequate to exclude the possibility that the distributions result from behavioural mechanisms which act to govern the observed larval and juvenile distributions, the observations on diel pattern of depth distribution provide little support for retention via diel vertical migration. The centres of mass for the nighttime distributions were only about 5 m deeper than those for the daytime distributions, and larval drift trajectories computed on the assumption of a diel migration between the observed time-varying currents (linearly interpolated from the moored measurements) were little different from those generated by assuming drift at the average depth of the centre of mass.

The observations point to significant interspecies and interannual variations in larval abundance and distribution, as well as persistent features within species from year to year. The plaice larvae were consistently associated with the relatively cool bottom water along the Bank's eastern edge. They were also more abundant in 1986 coincident with an increase in the distribution of cooler water on the Bank. These conditions arose from displacement of Labrador Current water onto the Bank in August 1986 during the most energetic (summertime) wind event of the three years. The associated increase in plaice abundance is consistent with the inferred advection of plaice southward along the bankward edge of the Labrador Current. Yellowtail distributions were qualitatively similar in the three years. However, witch distributions differed greatly, being more abundant in 1988 than in 1986 and 1987 without any unusual environmental conditions having been detected.

It appears that changes in spawning stock biomass can be dismissed as a cause for the large interannual differences in larval and juvenile densities. For yellowtail, research vessel surveys showed a decline in age 5+ abundance from 189 (millions) in 1986 to 168 and 98 and 1987 and 1988, respectively, while commercial catch rates indicated no change in stock status (Brodie et al. 1990b). In contrast, our larval surveys suggest the lowest densities during 1987 and approximately equal and much higher densities during 1986 and 1988. All indicators for plaice (research vessel surveys, catch rates, and sequential population models) indicate that there was no detectable change in adult abundance between 1986 and 1988 (Brodie et al. 1990a). Results from research vessel surveys for adult witch are inconclusive because of incomplete coverage of the expected distribution of adults (Bowering 1990b). However, commercial catch rates show a decline of about 40% between 1986 and 1988 (Bowering 1990b). If catch rates in the witch fishery are indicative of stock biomass, this implies a significant decline during this period, a result which contrasts with our ichthyoplankton surveys which yielded much higher catches of witch in 1988.

Overall, the larval distributions of plaice and yellowtail show similar patterns in the three years surveyed, apparently related to the bottom temperature variation across the southern Grand Bank. Although the mechanism underlying this temperature relation remains unclear, the available information on currents suggests that the distributions can be explained by passive advection, provided the larvae are in the lower water column and growth rates are close to maximum for yellowtail and close to minimum for plaice. Given the limited information available on vertical distributions of larvae and the horizontal structure of currents, it must be emphasized that this consistency does not exclude other scenarios requiring significant behaviour. The distribution of witch was not consistent in the three years (having a significant occurrence in only one year). There is more limited support for its distribution being consistent with passive advection, although it cannot be discounted.

Acknowledgements

We thank the many individuals who contributed to the execution of the field program. C. Ross made a major contribution to the physical oceanographic component, and J. McRuer, D. Reimer, and P. Vass made important contributions during the preparation and execution of the biological component. J. Simon, E. Dalley, R. Stone, L. Allen, B. McKenzie, C. Parsons, and H. Budgey also assisted during the program. M.-J. Graca assisted with the physical data analysis. This research was funded by the Department of Fisheries and Oceans, and by the Natural Sciences and Engineering Research Council of Canada through a Strategic Grant to W. C. Leggett.

References

BONNYMAN, S. 1983. Ichthyoplankton of the Grand Banks of Newfoundland. Grand Banks Oceanographic Study, Mobil Oil Canada, Ltd, St. John's, Nfld.

BOWERING, W. R. 1976. Distribution, age and growth, and sexual maturity of witch flounder (*Glyptocephalus cynoglossus*) in Newfoundland waters. J. Fish. Res. Board Can. 33: 1574–1584.

1990a. Spawning of witch flounder (*Glyptocephalus cynoglossus* L.) in the Newfoundland–Labrador area of the Northwest Atlantic as a function of depth and water temperature. Fish. Res. 9: 23–39.

1990b. Witch flounder in Divisions 3NO. NAFO SCR Doc. 90/54, Ser. No. N1775: 6 p.

BRODIE, W. B., W. R. BOWERING, AND J. W. BAIRD. 1990a. An assessment of the American plaice stock in Divisions 3LNO. NAFO SCR Doc. 90/80, Ser. No. N1802: 32 p.

BRODIE, W. B., S. J. WALSH, AND W. R. BOWERING. 1990b. Yellowtail flounder in NAFO Div. 3LNO — an assessment of stock status. NAFO SCR Doc. 90/86, Ser. No. N1812: 24 p.

CARSCADDEN, J. E., K. T. FRANK, AND D. S. MILLER. 1989. Capelin (*Mallotus villosus*) spawning on the Southeast Shoal: influence of physical factors past and present. Can. J. Fish. Aquat. Sci. 46: 1743–1754.

FAHAY, M. P. 1974. Occurrence of silver hake, *Merluccius bilinearis*, eggs and larvae along the middle Atlantic Continental shelf during 1966. Fish. Bull. 72: 813–830.

1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. Northwest Atl. Fish. Sci. 4: 423 p.

Fitzpatrick, C., and R. J. Miller. 1979. Review of spawning times and locations for some commercial finfish on the Newfoundland and Labrador coasts. Fish. Mar. Serv. Tech. Rep. 905: v + 14 p.

Frank, K. T., and J. E. Carscadden. 1989. Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic. J. Cons. Int. Explor. Mer 45: 146–164.

Greenberg, D. A., and B. Petrie. 1988. The mean barotropic circulation on the Newfoundland shelf and slope. J. Geophys. Res. 93: 15541–15550.

Hukuda, H., R. J. Greatbatch, and A. E. Hay. 1989. A simple three–dimensional model of the circulation off Newfoundland. J. Geophys. Res. 94: 12607–12618.

Loder, J. W. 1991. Summertime bottom temperatures on the Southeast Shoal of the Grand Bank, and implications for exchange rates. Can. J. Fish. Aquat. Sci. 48: 1316–1325.

Loder, J. W., and C. K. Ross 1988. Moored current and hydrographic measurements on the Southeast Shoal of the Grand Bank in 1986 and 1987. NAFO SCR Doc. 88/61, Ser. No. N1520: 21 p.

Loder, J. W., C. K. Ross, and P. C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic shelf. Can. J. Fish. Aquat. Sci. 45: 1860–1885.

McKenzie, R. A. 1955. Canadian Atlantic flounder fishery. Fish. Res. Board Can. MS Rep. 596.

Mountain, D. 1980. Direct measurements in the Labrador Current. J. Geophys. Res. 85: 4097–4100.

Myers, R. A., and K. F. Drinkwater. 1988. Ekman transport and larval fish survival. Biol. Oceanogr. 6: 45–64.

Nevinsky, M. M., and V. P. Serebryakov. 1973. American plaice, *Hippoglossoides platessoides* Fabr., spawning in the Northwest Atlantic area. Int. Comm. Northwest Atl. Fish. Res. Bull. 10: 23–36.

Petrie, B., S. Akenhead, J. Lazier, and J. Loder. 1988. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves, 1978–1986. NAFO Sci. Counc. Stud. 12: 57–69.

Petrie, B., and C. Anderson. 1983. Circulation on the Newfoundland continental shelf. Atmos.-Ocean 21: 207–226.

Pitt, T. K. 1966. Sexual maturity and spawning of the American plaice, *Hippoglossoides platessoides* (Fabricius), from Newfoundland and Grand Bank areas. J. Fish. Res. Board Can. 23: 651–672.

1970. Distribution, abundance, and spawning of yellowtail flounder, *Limanda ferruginea*, in the Newfoundland area of the Northwest Atlantic. J. Fish. Res. Board Can. 27: 2261–2271.

Ross, C. K., J. W. Loder, and M.-J. Graça. 1988. Moored current and hydrographic measurements on the Southeast Shoal of the Grand Bank, 1986 and 1987. Can. Data Rep. Hydrogr. Ocean Sci. 71: 132 p.

Sameoto, D. D., L. O. Jaroszynski, and W. B. Fraser. 1980. BIONESS, a new design in multiple net zooplankton samplers. Can. J. Fish. Aquat. Sci. 37: 722–724.

Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219: 731 p.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle, WA. 252 p.

Sinclair, M., and T. D. Iles. 1988. Population richness of marine fish species. Aquat. Living Resour. 1: 71–83.

Smigielski, A. S. 1979. Induced spawning and larval rearing of the yellowtail flounder, *Limanda ferruginea*. Fish. Bull. 76: 931–936.

Smith, W. G., J. D. Sibunka, and A. Wells. 1978. Diel movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete depth samplng. Fish. Bull. 76: 167–178.

Walsh, S. J. 1991. Commercial fishing practices on offshore juvenile flatfish nursery grounds on the Grand Banks of Newfoundland. Neth. J. Sea Res. 27: 423–432.

Wells, R., W. B. Brodie, C. A. Bishop, and J. W. Baird. 1988. Distribution and abundance of three fish species on the Grand Bank in relation to depth and temperature of the water. NAFO SCR Doc. 88/94, Ser. No. 1546: 26 p.

Wurtsbaugh, W. A., and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature (Lond.) 333: 846–848.

Zijlstra, J. J., R. Dapper, and J. Witte. 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea Res. 15: 250–272.

Recruitment of the 1987 Year Class of Georges Bank Haddock (*Melanogrammus aeglefinus*): The Influence of Unusual Larval Transport

T. Polacheck and D. Mountain

U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Woods Hole Laboratory, Woods Hole, MA 02543, USA

and D. McMillan, W. Smith, and P. Berrien

U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Sandy Hook Laboratory, Highlands, NJ 07732, USA

Polacheck, T., D. Mountain, D. McMillan, W. Smith, and P. Berrien. 1992. Recruitment of the 1987 year class of Georges Bank haddock (*Melanogrammus aeglefinus*): the influence of unusual larval transport. Can. J. Fish. Aquat. Sci. 49: 484–496.

Unusually strong along-shelf surface flow in the spring of 1987 transported haddock (*Melanogrammus aeglefinus*) larvae westward from spawning grounds on Georges Bank into the Middle Atlantic Bight, some as far as 400 km beyond the limits of their normal distribution. 0-Group haddock survived in the Bight in record numbers. Their center of abundance occurred along the outer half of the shelf from Delaware Bay to Martha's Vineyard where more than 97% of the 0-group fish resided in the fall of 1987. Juveniles remained more abundant in the Bight than on the bank through the spring of 1988. Collective evidence suggests that survivors returned to Georges Bank during the late spring/early summer of 1988. The estimated number of 0-group fish in the 1987 year class exceeded all previous estimates from a 27-yr time series which included the 1963 year class, the largest recruited to the fishery since record keeping began in 1931.

Un flot de surface fort et peu commun le long du plateau continental au printemps de 1987 a transporte larves d'aiglefin (*Melanogrammus aeglefinus*) en direction de l'ouest des frayeres du banc George jusque dans la Baie Mi-Atlantique, quelques aussi loin que 400 km au-dela des limites de leur repartition normal. Aeglefins de groupe 0 ont subsiste dans la baie a nombre record. Leur centre d'abondance avait lieu le long du moitie au large du plateau continental de la Baie Delaware jusqu'a l'isle de Martha's Vineyard ou au-dela de 97 % des poissons du group 0 demeuraient pendant l'automne de 1987. Les jeunes furent plus abondants dans la baie que sur le banc pendant toute la duree du printemps de 1988. Evidence collectif suggere que les survivants ont retourne au banc George pendant le printemps avance/ete debutante de 1988. Le nombre estime de poissons de groupe 0 de la classe de 1987 ont depasse toutes estimations prealables d'apres une serie temporel de 27 ans comprenant la classe annuel de 1963, la plus grande recrute a la peche depuis le temps qu'enregistrement fut etabli en 1931.

Received May 14, 1991
Accepted October 10, 1991
(JB036)

Reçu le 14 mai 1991
Accepté le 10 octobre 1991

Interest in the effects of transport mechanisms on the fate of fish eggs and larvae dates to the dawn of fishery science (Hjort 1914). Contemporary fishery biologists and oceanographers continue to pursue studies of advective processes, and many consider errant drift of spawning products to rank with predation and starvation as major factors in limiting year class success (Harden Jones 1968; Bailey 1981; Parrish et al. 1981). Because of the apparent dichotomy between the relatively low residence time of water on Georges Bank and its high but dramatically fluctuating fish production, the Bank has been the subject of studies to evaluate the influence of drift on the distribution and survival of fish eggs and larvae (Walford 1938; Chase 1955; Colton and Temple 1961; Bumpus 1976; Cohen et al. 1983). Although no one has previously demonstrated the mass transport of fish eggs and larvae of any species off Georges Bank, Mountain and Schlitz (1987) estimated that up to 50% of the zooplankton production on the bank might be lost through advective processes.

Sherman et al. (1984) reviewed the spawning strategies of selected coastal fishes in the Northeast Shelf Ecosystem. They concluded that species that spawn on Georges Bank depend on an anticyclonic gyre that dominates residual flow to hold the products of spawning on the bank. Smith and Morse (1985) and Lough and Bolz (1989) provided evidence to support Sherman et al. (1984) when they showed advective processes transporting haddock (*Melanogrammus aeglefinus*) larvae westward along the southern half of the Bank over depths between 50 and 100 m. Some larvae drifted west as far as Nantucket Shoals but most remained on the Bank.

In 1987, a dramatic change occurred in the seasonal distribution pattern of haddock larvae originating on Georges Bank, one that carried larvae several hundred kilometres south and west into the Middle Atlantic Bight. These transported larvae produced the largest number of recruiting 0-group haddock in the 27-yr history of the Northeast Fisheries Center's (NEFC) bottom trawl survey. This report tracks the unusual larval drift, describes the hydrographic conditions that caused it, and discusses the subsequent status of 0-group and juvenile haddock. To our knowledge, it provides (1) the first evidence of mass transport of fish larvae of any species off the bank and

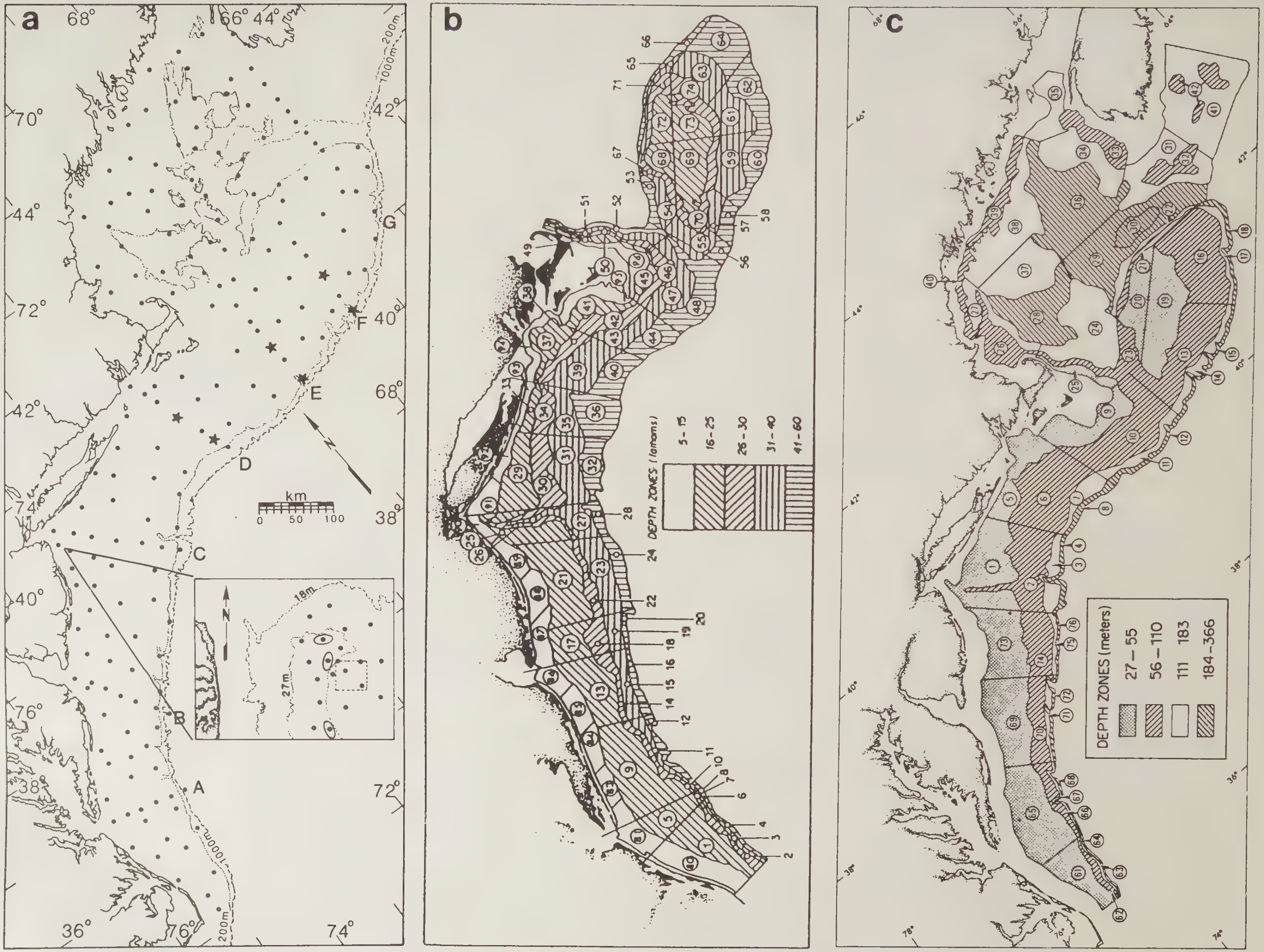

a
68°
66° 44°
70°
44°
72°
42°
74°
40°
76°
38°
36°
76°
74°
72°
38°
68°
40°
42°
200m
1000m
A
B
C
D
E
F
G
N
km
0 50 100
18m
27m
N
b
DEPTH ZONES (fathoms)
5 - 15
16 - 25
26 - 30
31 - 40
41 - 60
c
DEPTH ZONES (meters)
27 – 55
56 – 110
111 183
184-366

FIG. 1. (a) Standard MARMAP station plan. Station pairings used to calculate geostrophic current speed are noted with asterisks (*). Insert shows area and station density of the 12-Mile Dumpsite Recovery Study. Replicate tow stations are encircled with ellipses. (b) Strata sampled on NEFC scallop surveys. (c) Strata sampled on NEFC offshore bottom trawl surveys.

(2) plausible evidence that survivors of the 1987 year class returned to the bank during the summer of 1988.

Methods

Four research programs of the NEFC contributed to this document: (1) MARMAP (Marine Resources Monitoring, Assessment and Prediction), an 11-yr ecosystem monitoring program that included mesoscale collections of hydrographic data and fish eggs and larvae (Sherman 1980; Sibunka and Silverman 1984, 1989), (2) a 3-yr study in the New Year Bight Apex to document changes in the biomass of living marine resources during and after the cessation of sewage sludge dumping at the 12-Mile Dumpsite (Environmental Process Division 1988), (3) annual dredge surveys to assess the status of sea scallops (*Placopectin magellanicus*) off the northeastern United States (Serchuk and Smolowitz 1980), and (4) a 27-yr bottom trawl survey designed to assess coastal finfish populations in the Northeast Shelf Ecosystem (Grosslein 1969; Azarovitz 1981; Survey Working Group, NEFC 1988).

The MARMAP program comprised six to eight surveys each year in shelf waters from Cape Hatteras, NC, to Cape Sable, N.S. (Fig. 1). Temperature and salinity data were recorded from samples taken with water bottles and reversing thermometers on all MARMAP surveys except the final three in 1987 when an electric conductivity/temperature/depth profiling instrument (CTD) replaced the bottles. Manning and Lierheimer (1988), Holzwarth and Mountain (1990), and Mountain (1991) summarized MARMAP hydrographic observations. The accuracy of the data is at least ±0.02°C and ±0.02 PSU (practical salinity units). Temperature and salinity records from surveys during 1978–86 provide a basis for identifying unusual aspects of conditions in 1987, the final year of survey activity. For this report, the along-shelf surface geographic current is calculated for all spring occupations of selected station pairs on three cross-shelf sections: the southern flank of Georges Bank, Great South Channel, and the shelf south of Narragansett Bay (Fig. 1a). These estimates of currents provide an index of the interannual variability in the flow of water from Georges Bank into the Middle Atlantic Bight.

Haddock eggs and larvae were collected on MARMAP surveys with a 61-cm bongo fitted with a 0.505-mm-mesh net. To estimate larval advection rates, lengths of specimens <16 mm are corrected for shrinkage using information in Morse (1984), and then all lengths are converted to age based on Bolz and Lough (1988). Because haddock eggs float near the surface (Miller et al. 1963), we use estimated mean temperatures in surface to 15-m depths at the time of hatching (see Mountain 1989) and information from Hardy (1978) and Laurence and Rogers (1976) to derive incubation periods. The incubation time is added to the age of each larva to determine its spawning date, the date used to estimate distance travelled and area of origin. For this exercise, spawning locations are assumed to be where egg concentrations were observed in February, April, and May.

The 12-Mile Dumpsite Recovery Study, scallop surveys, and bottom trawl surveys each contributed different information on young-of-the-year and juvenile haddock which reflects the differences in sampling design and gear among the three surveys. The dumpsite study, which alternated monthly between sampling a series of 22 fixed stations in the vicinity of the dumpsite and replicate sampling at selected stations (Fig. 1a), provided the most detailed temporal resolution of the presence/absence of 0-group and juvenile haddock in the Middle Atlantic Bight with monthly samples throughout the year. The scallop and bottom trawl surveys use stratified random sampling designs which cover the entire U.S. northeast shelf region (Fig. 1b and 1c). The summer scallop survey provided the earliest information on the spatial distribution of newly recruited 0-group haddock, while the fall and spring bottom trawl surveys provided the most extensive temporal/spatial coverage after larvae settled to the bottom.

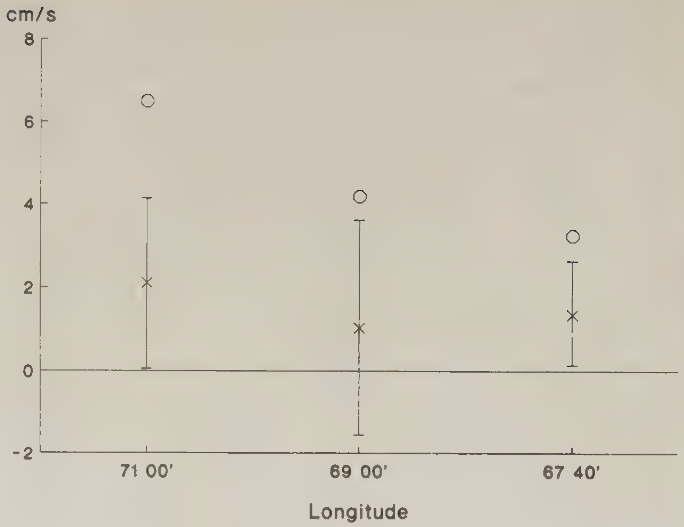


FIG. 2. Westward geostrophic current speed on the outer continental shelf at three longitudes during spring. Open circles (○) represent 1987 values; ×'s represent the mean of estimated current values for years 1978–86. Bars indicate ±1 standard deviation about the mean.

The fish fauna at the dumpsite was sampled with 15-min tows using an otter trawl with a 9.75-m (32-ft) headrope, a 11.0-m (36-ft) footrope without rollers, and a 5-cm (2-in.) mesh cod end. The NEFC scallop surveys use 15-min tows and a 2.44-m (8-ft) dredge with a 5-cm (2-in.) chain bag lined with 3.8-cm (1.5-in.) stretch mesh webbing. Although not designed for catching fish, this scallop dredge regularly captures juveniles of several species, and information on the fish caught has been included in the computerized data base since 1986. The trawl survey fishes for 30 min with a 36 Yankee trawl with roller gear and a 1.27-cm (0.5-in.) mesh cod end liner.

Indices of abundance calculated from the NEFC bottom trawl surveys are used routinely as part of the assessment of the Georges Bank haddock stock. Age-specific indices for young-of-the-year and juvenile haddock provide good estimates of year class strength (see Clark et al. 1982; Overholtz et al. 1983; Gravaris 1988). The stock area routinely used for haddock assessments encompasses strata in the Georges Bank/southern Gulf of Maine/Nantucket Shoals area, e.g. strata 13–25, 29, and 30 in Fig. 1c. Strata west of Georges Bank traditionally have been considered peripheral to the distribution of haddock and they have not been included in assessments. In this paper, we recognize the traditional Georges Bank stock area plus two other areas: western Nantucket Shoals, or strata 9–12, and the Middle Atlantic Bight, strata 1–8 and 69–76 (Fig. 1c). The corresponding strata for the scallop survey are 49–74 for Georges Bank, 37–44 for Nantucket Shoals, and 13–40 for the Middle Atlantic Bight (Fig. 1b).

Results

Hydrography

Near-normal water temperature and salinity conditions prevailed in the Georges Bank area in the spring of 1987 but

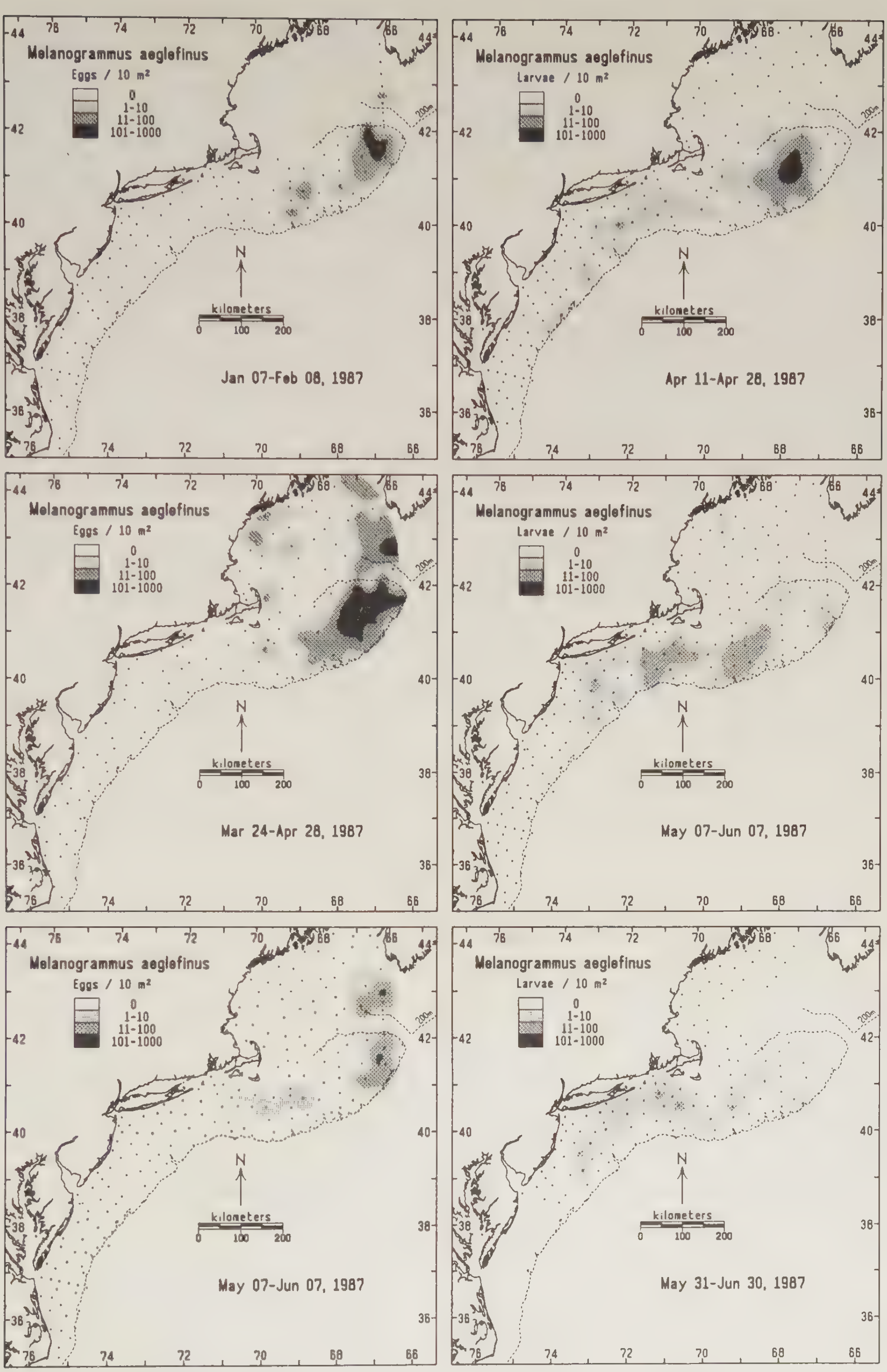

Melanogrammus aeglefinus
Eggs / 10 m²
Larvae / 10 m²
0
1-10
11-100
101-1000
200m
N
kilometers
0
100
200
Jan 07-Feb 08, 1987
Apr 11-Apr 28, 1987
Mar 24-Apr 28, 1987
May 07-Jun 07, 1987
May 07-Jun 07, 1987
May 31-Jun 30, 1987
76
74
72
70
68
66
44
42
40
38
36

FIG. 3. Distribution of haddock eggs (left) and larvae (right) from 1987 MARMAP surveys.

westward-flowing geostrophic currents at the three cross-shelf station pairings were the highest of the 11-yr MARMAP time series. At each of the three longitudinal sections, the 1987 estimate was more than twice the mean and more than 1 standard deviation above the means for the other years (Fig. 2). Mountain (1991) showed that the volume of shelf water in the Middle Atlantic Bight in the spring of 1986 was 1500 km^3 below normal; by the end of 1987, it increased to a level 1500 km^3 above normal. He attributed this dramatic change to increased flow through the entire Northeast Shelf ecosystem, i.e. the Gulf of Maine to Georges Bank and westward into the Middle Atlantic Bight. To transport an additional 3000 km^3 of water through the system over the 16-mo period would require an increase in flow of about 0.07×10^6 m^3/s, or a 20% increase in the mean along-shelf transport.

Warm slope water usually encroaches shoreward over the bottom off southern New England in autumn and bottom temperatures on the outer half of the shelf reach their annual peak (Mountain and Holzwarth 1990). In the autumn of 1987, the unusually large volume of shelf water in the Middle Atlantic Bight prohibited the encroachment of warm slope water onto the shelf and bottom temperatures were 2–4°C below normal (Manning and Lierheimer 1988). This event held bottom temperatures within the tolerance range of 0-group haddock and might have been critical to their survival in the Bight during the autumn period.

Eggs and Larvae

We caught haddock eggs and larvae on MARMAP surveys from February through June 1987. The spatial/temporal distribution patterns of eggs resembled those described by Smith and Morse (1985) for the initial 6 yr of the MARMAP program. Eggs first occurred in samples taken in early February, abundance peaked in mid-April when eggs covered most of Georges Bank, and production was sharply curtailed as the spawning season came to a close after mid-May. Although the center of spawning activity remained over the eastern part of Georges Bank throughout the 1987 spawning season, spawning persisted at a reduced level on Nantucket Shoals. No haddock eggs were collected west of the shoals (Fig. 3).

We first observed evidence of unusual larval drift in April when 35% of the haddock larvae in MARMAP collections occurred west of Nantucket Shoals. Although the center of larval abundance remained on Georges Bank, somewhat west of the principal spawning grounds, we caught haddock larvae along the outer half of the shelf as far west and south as Virginia. This represents the southernmost occurrence of recently spawned haddock in the entire 11-yr MARMAP time series (Fig. 3).

The pattern of significant westward displacement continued in May when 25% of the captured haddock larvae occurred west of Nantucket Shoals. Only broken, low-density patches of larvae occurred in May over the eastern half of Georges Bank, the center of spawning activity throughout the late winter/spring period. By June, 57% of the haddock larvae from MARMAP ichthyoplankton collections had drifted into shelf waters of the Middle Atlantic Bight. Survey coverage did not include eastern Georges Bank in June but, based on evidence in May, there is no reason to suppose that we failed to sample a major concentration of haddock larvae on the eastern half of Georges Bank (Fig. 3). By July, young haddock were demersal and they began to show up in trawl samples taken near the 12-Mile Dumpsite and in the annual scallop survey.

TABLE 1. Calculated mean drift rates of haddock larvae from longitudinal midpoints of egg distribution to longitudinal midpoints of catch locations in 1987. Drift was assumed to be from east to west. Rates <10 cm/s were considered to reflect possible spawning areas.

		Capture location								
		Middle Atlantic Bight			Nantucket Shoals			Georges Bank		
Capture month	Spawning location	74°	73°	72°	71°	70°	69°	68°	67°	66°
Mean age (d (N))										
April		48.0(1)	49.0(4)	40.0(12)	33.2(16)	31.8(6)	29.0(4)	24.2(8)	25.4(36)	25.1(8)
Mean drift rate (cm/s)										
	70°	8.96	6.78	5.58	3.63	—	—	—	—	—
	69°	10.48	8.43	7.66	6.77	3.34	—	—	—	—
	68°	12.93	10.87	10.59	10.06	6.46	3.76	—	—	—
	67°	14.92	12.68	12.98	13.20	9.73	7.05	3.89	—	—
	66°	17.03	14.92	15.32	16.32	12.90	10.96	7.52	4.29	—
Mean age (d (N))										
May		No data	50.3(4)	48.6(7)	44.1(24)	38.2(5)	37.8(29)	39.6(29)	40.0(1)	30.4(8)
Mean drift rate (cm/s)										
	70°	—	6.63	5.06	2.72	—	—	—	—	—
	69°	—	8.18	6.88	4.86	2.75	—	—	—	—
	68°	—	10.47	9.23	7.34	5.03	2.85	—	—	—
	67°	—	12.39	11.56	9.75	8.03	5.51	2.90	—	—
	66°	—	14.33	13.51	11.94	10.60	8.30	5.71	2.60	—
Mean age (d (N))										
June		No data	81.8(8)	63.2(12)	50.7(4)	47.8(8)	45.4(6)	56.2(4)	No data	No data
Mean drift rate (cm/s)										
	70°	—	4.01	3.68	2.31	—	—	—	—	—
	69°	—	5.13	5.16	4.16	2.26	—	—	—	—
	68°	—	6.49	6.87	6.20	4.37	1.98	—	—	—
	67°	—	7.65	8.48	8.23	6.59	4.14	1.97	—	—
	66°	—	8.96	10.03	10.14	8.77	6.24	3.82	—	—

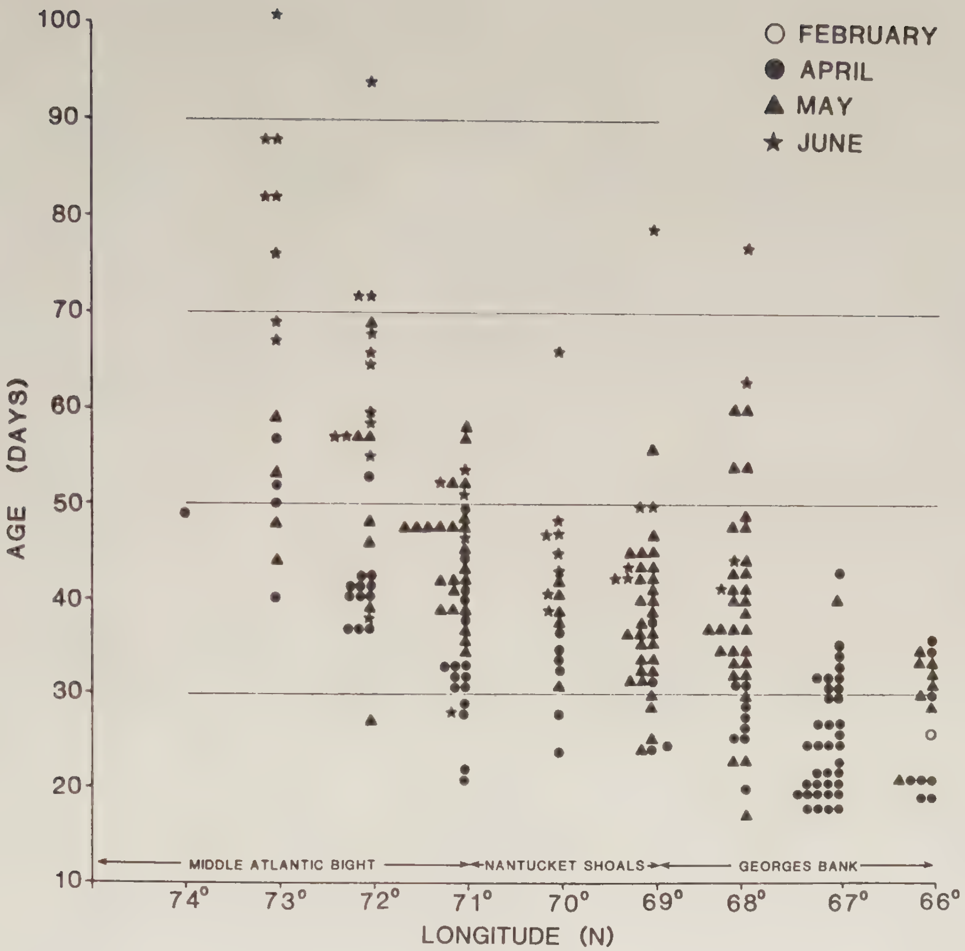


FIG. 4. Estimated ages and catch locations of haddock larvae from 1987 MARMAP surveys depicting their westward displacement over time.

Determining precise spawning locations of larvae caught west of Nantucket Shoals is beyond the scope of our data base. To estimate the potential areas of origin, we measured straight-line drift from longitudinal midpoints of the known spawning areas on Georges Bank and Nantucket Shoals to capture locations in the Middle Atlantic Bight. While the geostrophic current estimates in Fig. 2 provide a relative index of variability, they do not give an absolute measure of velocity. Instead, based on monthly mean flow at middepths along the southern flank of Georges Bank in spring (Butman et al. 1987) and information on the vertical distribution of young haddock (Colton and Temple 1961), we considered transport rates of 5–10 cm/s to be representative of normal conditions. Calculated drift rates for larvae caught in April, May, and June are listed in Table 1 to determine potential locations of origin.

Larvae caught at the western limit of their distribution in April, i.e. within the 73° meridian, ranged in age from 42 to 58 d (Fig. 4). Excessively high transport rates of 12.3–17.0 cm/s would have been required for these larvae to reach their capture site from the primary spawning grounds on eastern Georges Bank. More realistic rates of 5.5–8.0 cm/s could have transported them to the area of capture from the secondary spawning area on western Georges Bank (see Fig. 3). Those caught on the shoals probably originated on Georges Bank but not the extreme eastern part of the bank (Table 1). Given the egg distribution patterns in February and April (Fig. 3) and the calculated ages and drift rates of larvae in Table 1, we concluded that larvae caught in the Middle Atlantic Bight in May originated on the western half of Georges Bank. Those caught in the bight in June could have been spawned over the eastern part of the bank.

Although our 1987 results show nothing unusual in the spatial/temporal distribution of haddock eggs, the spring larval distribution patterns in 1987 differ markedly from those observed in other years of the 11-yr MARMAP program, with the exception of 1977. We caught larvae as far west as eastern Long Island in two other years, 1977 and 1979. During the remaining eight years, they were taken largely within the Georges Bank/Nantucket Shoals area. Significant numbers of larvae occurred west of Nantucket Shoals in only two years. In 1977, 27% of the larvae in our samples occurred west of the 71° meridian and in 1987 we found 38% west of 71°. Less than 1% occurred west of Nantucket Shoals in 1979, 1980, and 1983, while 4% drifted into the Middle Atlantic Bight in 1984. None were caught west of 71° in 5 of the 11 years (Fig. 5).

Young-of-the-Year

Newly recruited haddock from the 1987 year class were first detected during the 12-Mile Dumpsite Recovery Study and the NEFC scallop survey in July, the month after they last occurred in plankton samples. Fourteen 0-group haddock occurred in trawl collections near the dumpsite (Fig. 6). The scallop survey produced a stratified mean catch per tow of 1.25 in the Middle Atlantic Bight compared with 0.08 for Georges Bank. In the Middle Atlantic Bight, 0-group haddock occurred in strata from Delaware Bay to the eastern tip of Long Island in depths from

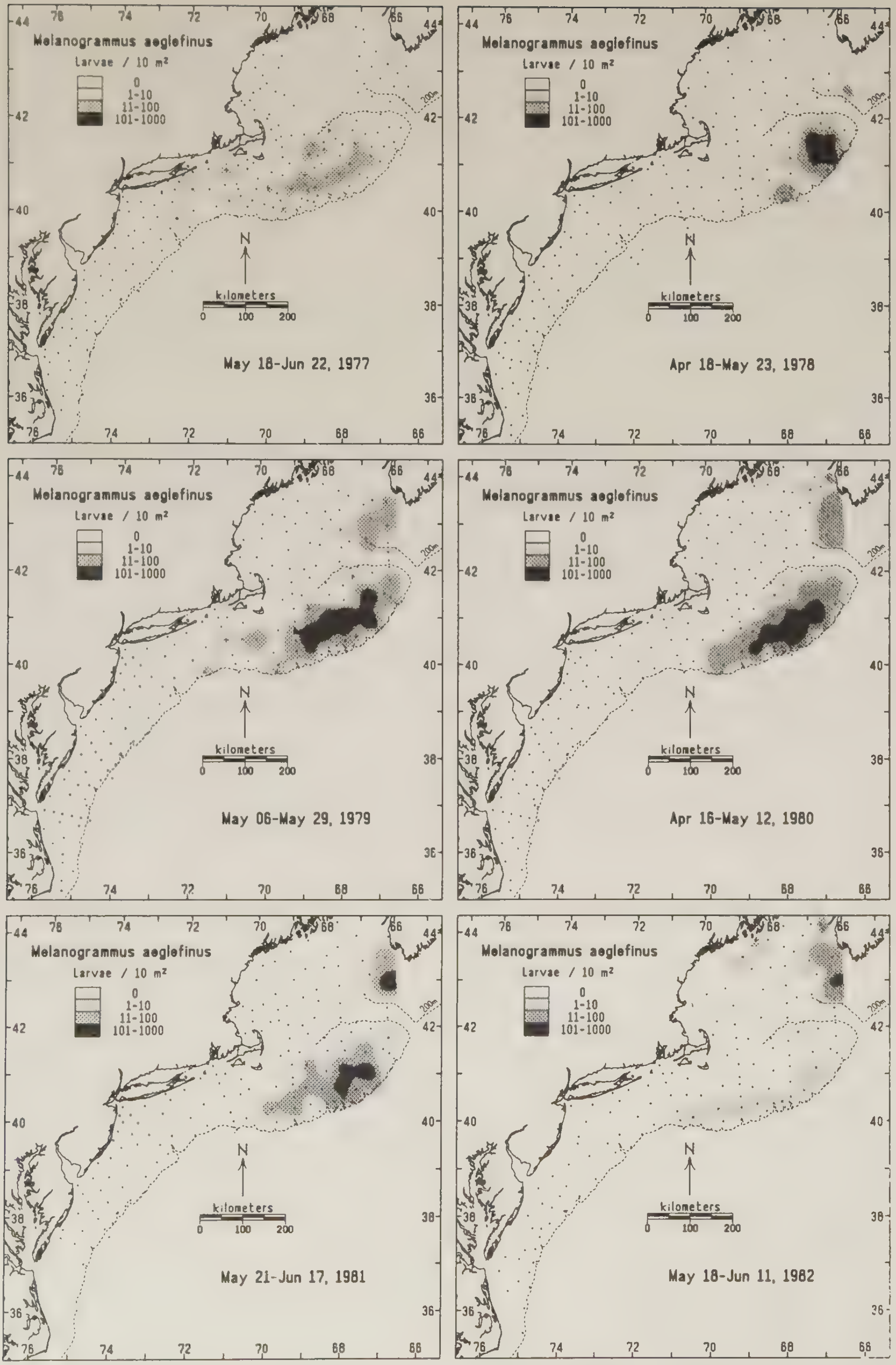

Melanogrammus aeglefinus
Larvae / 10 m²
0
1-10
11-100
101-1000
N
kilometers
0
100
200
200m
May 18-Jun 22, 1977
Apr 18-May 23, 1978
May 06-May 29, 1979
Apr 16-May 12, 1980
May 21-Jun 17, 1981
May 18-Jun 11, 1982
44
42
40
38
36
76
74
72
70
68
66

FIG. 5. Distribution of haddock larvae in spring 1977–87 comparing the relative extent of westward transport in 1987 with other years. (*Fig. 5 continued next page*)

27 to 73 m (15 to 40 fathoms) (Table 2). None occurred around Nantucket Shoals. With only a limited time series of data on 0-group haddock available from the scallop surveys, we have little basis for evaluating the significance of the large difference in the relative catch rates between Georges Bank and the Middle Atlantic Bight. However, the results provide the first evidence that a relatively large percentage of the larvae that drifted into the Bight successfully settled out of the plankton. Furthermore, the difference in relative abundance of 0-group fish in the two areas suggests that most of the recruitment from the 1987 spawning season occurred in the Middle Atlantic Bight.

The autumn bottom trawl survey confirmed results of the scallop survey with respect to the principal location of recruitment. The density of 0-group haddock in the Middle Atlantic Bight exceeded by 40 times that found on Georges Bank, with greatest numbers occurring along the outer half of the shelf from Delaware Bay to Martha's Vineyard (Table 3). Calculations of the sum of the product of the mean density times the

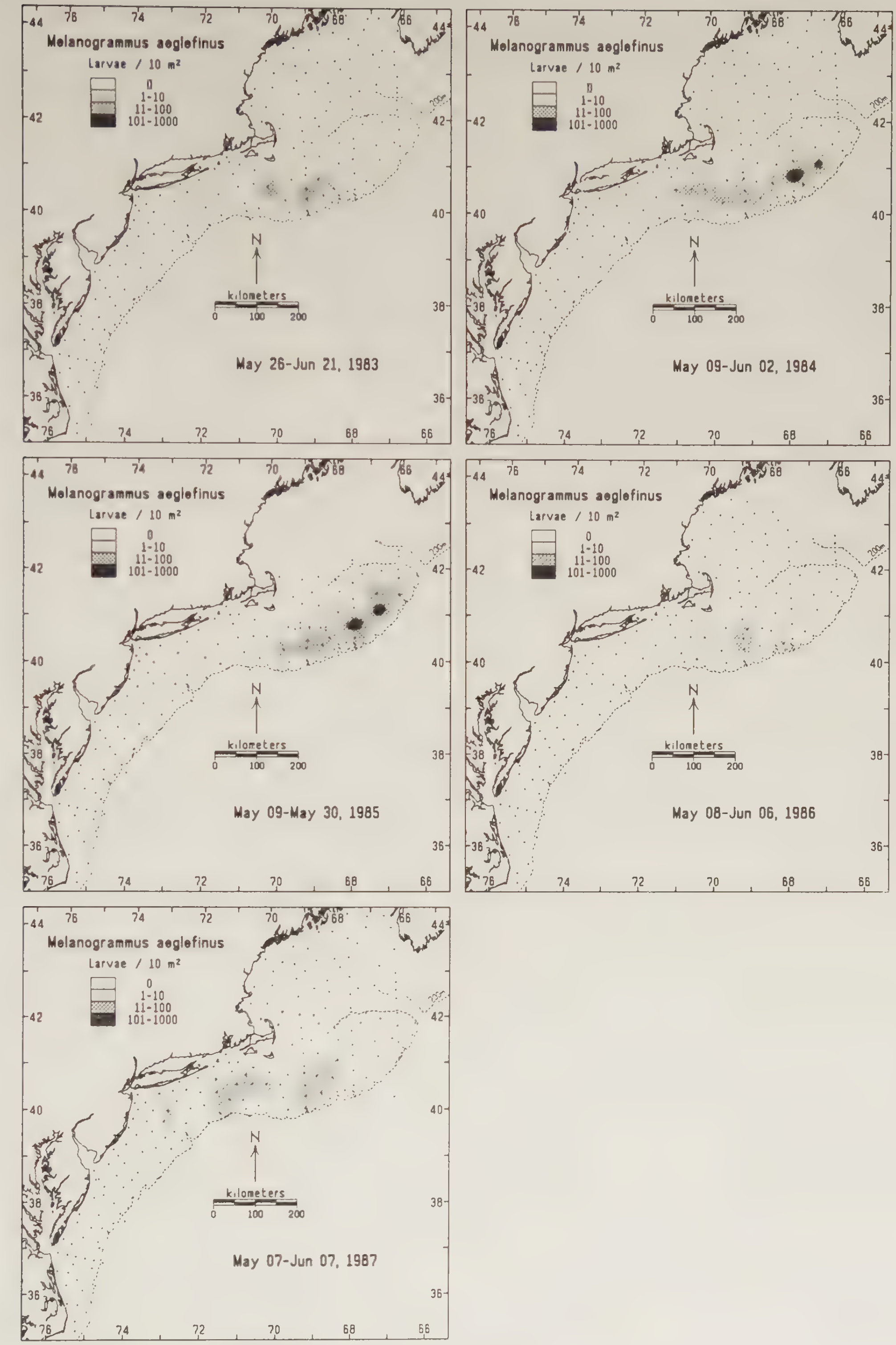

Melanogrammus aeglefinus
Larvae / 10 m²
0
1-10
11-100
101-1000
N
kilometers
0 100 200
200m
May 26-Jun 21, 1983
May 09-Jun 02, 1984
May 09-May 30, 1985
May 08-Jun 06, 1986
May 07-Jun 07, 1987
44
42
40
38
36
76
74
72
70
68
66

FIG. 5. (*Concluded*)

area for each stratum holding 0-group haddock revealed that an estimated 97% of the 1987 year class occurred in the Middle Atlantic Bight in the autumn of 1987. Only 2.6% resided within the traditional Georges Bank region and 0.3% in the western Nantucket Shoals area.

The 0-group haddock within the Georges Bank region tended to concentrate along the eastern edge of Nantucket Shoals in stratum 25 where their density was nearly nine times greater than in any other stratum on the bank. Based on area and mean density, stratum 25 accounted for 60% of the recruits within the immediate Georges Bank area. With the exception of 1987, this stratum never accounted for more than 30% of the 0-group haddock, and only in three years, 1963, 1975, and 1984, did the percentage exceed 10%.

Interannual comparisons of trawl survey results indicate that the density of 0-group haddock in the Middle Atlantic Bight in 1987 exceeded that found on Georges Bank during the entire 27-yr time series (Table 4). Taking into account the relative areas of the strata and the abundance of 0-group haddock, we estimate that the total number of fish in the 1987 year class

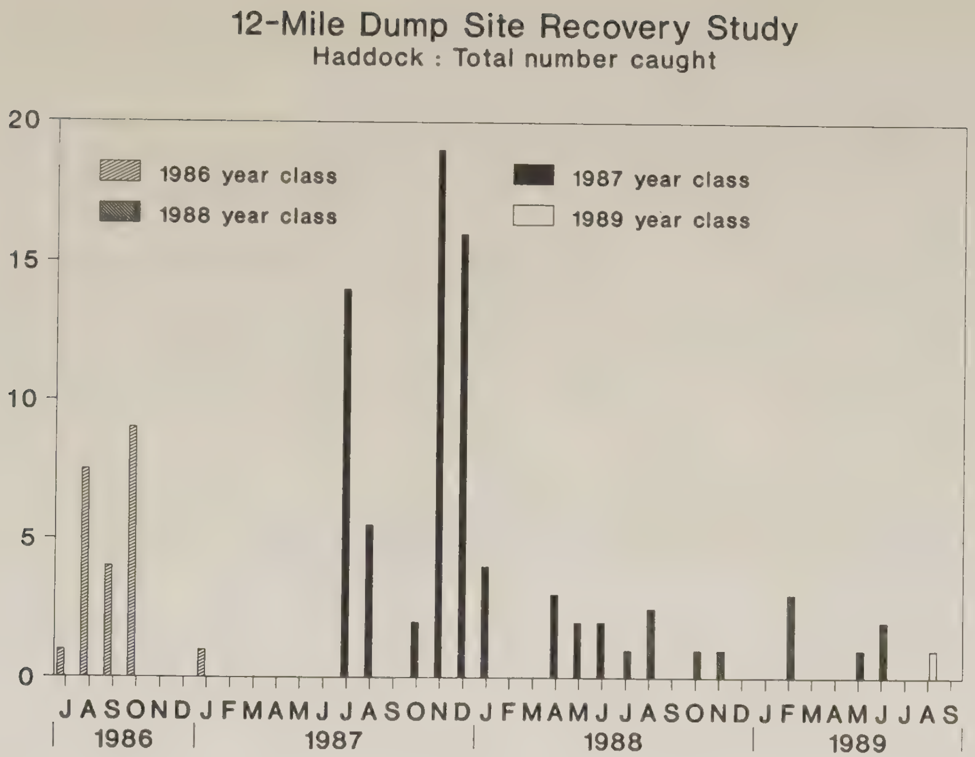


FIG. 6. Occurrence of 0-group and juvenile haddock near the 12-Mile Dumpsite Recovery Study, 1986–89.

exceeded all previous year classes in the time series. The abundance estimate is similar to that observed in 1963, a year class estimated by Clark et al. (1982) and Gravaris (1988) to be 2.5 times larger than any recruited into the fishery since the recording of adequate catch-at-age statistics began in 1931 (Fig. 7).

A further review of the bottom trawl time series reveals that the Middle Atlantic Bight held a significant fraction (>50%) of 0-group haddock in 6 of 27 years. In three of the six years, recruitment throughout the Georges Bank and Middle Atlantic Bight areas was extremely poor, with the mean number of 0-group fish being less than 0.1/tow. The occurrence of 0-group haddock in the Middle Atlantic Bight during these years was of little significance. In the other three years, 1965, 1971 and 1988, the mean catch exceeded 0.5/tow and the significance of the catch in the Bight is less clear.

Monthly sampling near the 12-Mile Dumpsite showed that 0-group haddock remained in the Middle Atlantic Bight through the autumn of 1987 and winter of 1988 (Fig. 6). Although 0-group and juvenile haddock occurred near the 12-Mile Dumpsite in all three years of the study, representatives of the 1987 year class exceeded those of the other two years by more than a factor of 2.

Juveniles

Most of the 1987 year class remained in the Middle Atlantic Bight through the spring of 1988. Catch per tow on the spring trawl survey averaged 2.36 in the Bight and 1.55 on Georges Bank. While these numbers suggest higher winter mortality in the Bight than on the Bank, the results indicate that 58% of the survivors remained well to the west of their normal distribution. Relatively high densities of age 1 haddock occurred off Long Island in strata 2, 5, and 6 (Table 3). Strata 2 and 6, which cover the outer half of the shelf, held high densities the previous fall. Only scattered occurrences of age 1 fish occurred off southern New Jersey, where high densities of 0-group fish resided during the autumn of 1987. On Georges Bank, survivors of the 1987 year class were most abundant in depths >50 m along the southwestern flank in stratum 13 (Table 3). None occurred in stratum 25, an area of high abundance the previous autumn.

Haddock from the 1987 year class continued to occur near the 12-Mile Dumpsite through June 1988 (Fig. 6). We assume that this date approximates the end of their widespread distribution in the Middle Atlantic Bight, as none occurred thereafter in the dumpsite study, the summer scallop survey, or the autumn trawl survey. In contrast, increased abundance levels of age 1 haddock on Georges Bank in 1988 suggest that an immigration of fish from the 1987 year class took place. Interannual comparisons of mean catch per tow between 1987 and 1988 from the scallop surveys revealed that catches on the Bank increased by more than a factor of 2, while the relative abundance index from the bottom trawl surveys increased by 1.95 between the spring and autumn of 1988. The 1988 autumn trawl value of 3.02 fish/tow represents the ninth largest for any year class at this age in the 27-yr time series. Subsequent results from both the spring and autumn 1989 trawl survey and catch statistics from the fishery further confirm the relative strength of the 1987 year class on Georges Bank.

Discussion

Differences in the locations of haddock eggs and larvae, the westward shift in larval distribution patterns over time, and the unusually strong geostrophic current estimates in the spring of 1987 collectively provide the most conclusive evidence yet reported for the mass transport of fish larvae off Georges Bank. Although we considered drift rates >10 cm/s excessively high, given the exceptional 1987 hydrographic conditions, they might not have been. It should be noted that even the most extreme

TABLE 2. Mean catch per tow of age 0 haddock during the NEFC 1987 summer scallop dredge survey by stratum and region (see Fig. 1b).

Middle Atlantic Bight			Nantucket Shoals			Georges Bank		
Stratum	Number of tows	Mean number per tow	Stratum	Number of tows	Mean number per tow	Stratum	Number of tows	Mean number per tow
13	3	0.00	37	4	0.00	49	9	0.00
14	12	7.01	38	6	0.00	50	16	0.00
15	11	0.18	39	3	0.00	51	11	0.09
16	7	0.00	40	2	0.00	52	11	0.00
17	1	3.00	41	3	0.00	53	7	0.00
18	10	5.30	42	3	0.00	54	7	0.00
19	12	0.15	43	2	0.00	55	9	0.56
10	3	0.33	44	3	0.00	56	3	0.00
21	2	1.50	45	3	0.00	57	3	0.00
22	8	2.13	46	6	0.00	58	8	0.13
23	16	0.19	47	12	0.08	59	12	0.00
24	4	0.50	48	8	0.00	60	12	0.00
25	4	7.20				61	8	0.13
26	14	3.50				62-1	12	0.00
27	20	1.10				62-2	6	0.00
28	10	0.00				63-1	7	0.00
29	6	0.00				63-2	8	0.00
30	15	1.93				64	16	0.00
31	24	2.92				65-1	12	0.18
32	4	0.00				65-2	10	0.00
33	10	1.10				66-1	12	0.00
34	14	1.00				66-2	8	0.00
35	10	0.40				71	5	0.00
36	2	0.00				72	6	0.00
37	4	0.00				73	6	0.00
38	6	0.00				74	8	0.13
39	3	0.00						
40	2	0.00						
Regional stratified mean number per tow		1.25			0.01			0.06

drift rates calculated in Table 1 fall within recorded mean current rates on Georges Bank, and 96% are within or below typical near-surface current speeds of 10–15 cm/s reported from the southern flank of Georges Bank by Butman et al. (1987). At this near-surface rate of transport, larvae caught in April and May in the Middle Atlantic Bight could have originated on the primary spawning grounds over eastern Georges Bank.

Smith and Morse (1985) and Lough and Bolz (1989) reported a westward displacement of haddock larvae on Georges Bank, with most eventually moving toward the shallow central part of the Bank. Smith and Morse found little evidence of transport off the Bank and no evidence of larvae moving onto the Bank from the Scotian Shelf or Gulf of Maine. They reported only scattered occurrences of pelagic larvae west of Nantucket Shoals and concluded that most of those that escaped the influence of the Georges Bank gyre drifted past Great South Channel and found their way onto Nantucket Shoals. Contrary to their results, Walford (1938) reported catching more than 600 haddock larvae in the Middle Atlantic Bight in 1931 and 1932, with most occurring in the second year of his 2-yr study. He estimated drift rates between May and June of 1932 at 2 mi/d (4.16 cm/s) which is less than that used in our study.

Our collective studies clearly show that both larvae and 0-group haddock of the 1987 year class occurred in the Middle Atlantic Bight at the highest abundance levels ever recorded. Despite this indisputable evidence, the presence of 0-group haddock near the 12-Mile Dumpsite in all three years of the study suggests that the occurrence of haddock in the Bight, at least in small numbers, might be more common than indicated by the bottom trawl time series. Lough et al. (1989) attributed the undersampling of 0-group gadids on NEFC bottom trawl surveys to the use of large rollers on the footrope.

The fate of haddock from the 1987 year class that survived until spring 1988 in the Middle Atlantic Bight is critical in attempting to evaluate the significance of westward drift in the overall recruitment process for Georges Bank haddock. If age 1 haddock from the Middle Atlantic Bight never return to Georges Bank, they are little more than biological curiosities. In this case, westward transport off the Bank would have a negative effect on year class success. On the other hand, if substantial numbers of juveniles from the 1987 year class returned to Georges Bank, as we suspect, then a degree of plasticity exists in what constitutes suitable nursery habitat for this stock, and remaining within the influence of the Georges Bank gyre is not critical for survival.

TABLE 3. Stratified mean catch per tow of 1-yr-old haddock during the fall 1987 and spring 1988 NEFC bottom trawl surveys by stratum and region (see Fig. 1c).

		Number of tows		Mean number per tow		Mean number per tow for a region	
Region	Stratum	Fall	Spring	Fall	Spring	Fall	Spring
Middle Atlantic Bight	1	7	7	7.14	0.00	71.44	2.36
	2	7	7	368.14	8.71		
	3	2	2	0.00	0.00		
	4	1	1	0.00	0.00		
	5	5	6	5.80	3.17		
	6	8	8	112.75	6.63		
	7	2	2	0.00	0.00		
	8	1	1	0.00	0.00		
	69	6	6	0.00	0.00		
	70	4	4	0.25	0.00		
	71	2	3	0.00	0.00		
	72	1	0	0.00	—		
	73	5	5	0.00	0.60		
	74	4	4	138.50	0.25		
	75	2	2	0.00	0.00		
	76	1	1	0.00	0.00		
Nantucket Shoals	9	5	5	0.00	0.00	0.88	0.27
	10	8	8	1.63	0.50		
	11	2	2	0.00	0.00		
	12	1	1	0.00	0.00		
Georges Bank	13	10	9	0.00	10.11	1.80	1.55
	14	3	3	0.00	0.00		
	15	1	1	0.00	0.00		
	16	10	10	0.70	1.00		
	17	3	3	0.33	0.00		
	18	2	1	0.00	0.00		
	19	9	9	0.56	0.11		
	20	6	6	0.50	0.00		
	21	4	4	0.50	0.50		
	22	4	4	0.00	0.00		
	23	5	4	6.00	1.25		
	24	6	6	1.17	0.00		
	25	3	4	53.00	0.00		
	29	8	9	0.00	0.11		
	30	3	3	0.00	0.00		

Our data set does not allow us to definitely determine whether any juvenile haddock from the 1987 year class emigrated from the Middle Atlantic Bight to Georges Bank. However, collective evidence described in this report, i.e. the high numbers of larvae, 0-group, and juveniles in the Bight and their low numbers on the Bank in the summer and autumn of 1987, followed by the reversal in this pattern in the autumn of 1988, suggests that an exodus from the Bight to the Bank took place. We consider it unlikely that mortality rates in the Bight could increase to nearly 100% as absence of juveniles in summer and autumn 1988 collections might suggest. Finally, the stratified mean catch per tow from trawl tows on Georges Bank increased by a factor of 1.95 between spring and autumn of 1988. While increases of similar magnitude occurred in other years when we have no evidence of large numbers of 0-group fish in the Bight, the 1988 increase supports our hypothesis that juvenile haddock emigrated from the Middle Atlantic Bight to Georges Bank.

To support our hypothesis, we considered several factors that might have adversely influenced the survival of haddock in the Middle Atlantic Bight during the summer of 1988. It seems unlikely that temperature can be implicated. Summer bottom water temperatures over the outer half of the shelf off Long Island, i.e. strata 2 and 6, fell within the 6–12°C range associated with haddock on Georges Bank (Mountain and Holzwarth 1990). Furthermore, summer temperatures at the 12-Mile Dumpsite were the coldest recorded during the 3-yr study (Environmental Process Division 1992) and within the tolerance limits of haddock.

Food requirements are also unlikely to be a major factor in limiting survival in the Bight, as both 0-group and juvenile haddock have variable diets. Lough et al. (1989) reported that 0-group haddock rise off the bottom to feed at night. Their diet consists largely of amphipods and euphausids, while haddock >8 cm turn to the benthos, i.e. amphipods, decapods, and polychaetes (Bowman 1981). Haddock increased in mean size from 7 cm in July 1987 to 28 cm in June 1988 near the 12-Mile Dumpsite and from 14 to 21 cm between the autumn 1987 and spring 1988 trawl survey. These growth rates are consistent with rates reported for haddock on Georges Bank and further indicate that food would not limit survival in the Bight. Finally, bottom type where haddock occurred in the Middle Atlantic Bight, largely sand and gravel (Freedland and Swift 1978), resembles that where Lough et al. (1989) observed 0-group haddock most abundant on Georges Bank. Based on the above, limitations of food, temperature, and habitat provide an unacceptable explanation for the disappearance of age 1 haddock from the bight during the summer of 1988.

TABLE 4. Stratified mean catch per tow of age 0 haddock during the NEFC fall bottom trawl by year and region.

Year	Middle Atlantic Bight	Nantucket Shoals	Georges Bank
1963	0.00	0.30	54.85
1964	0.55	3.96	2.76
1965	1.06	0.00	2.24
1966	0.00	0.00	4.06
1967	0.03	0.00	0.00
1968	0.00	0.00	0.07
1969	0.01	0.00	0.23
1970	0.06	0.00	0.00
1971	1.88	0.04	1.59
1972	0.00	0.00	4.47
1973	0.00	0.00	2.15
1974	0.00	0.07	0.46
1975	0.02	0.18	15.27
1976	0.00	0.00	2.89
1977	0.00	0.00	0.05
1978	0.06	0.07	10.89
1979	0.01	0.00	1.07
1980	0.08	0.00	9.56
1981	0.00	0.00	0.29
1982	0.00	0.00	0.89
1983	0.00	0.00	2.24
1984	0.08	0.00	0.02
1985	0.02	0.20	7.12
1986	0.00	0.00	0.00
1987	71.44	0.88	1.78
1988	0.54	0.00	0.62
1989	0.09	0.00	0.37

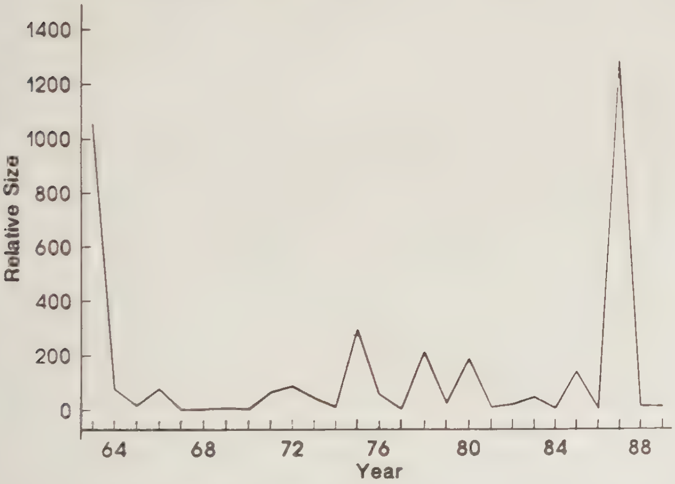


FIG. 7. Relative abundance (stratified mean number per tow times area) of 0-group haddock caught in the NEFC trawl survey for Georges Bank, Nantucket Shoals, and Middle Atlantic Bight, 1963–89.

Our conclusion that haddock larvae that drift into the Middle Atlantic Bight can survive and return to Georges Bank contrasts with that of Walford (1938). He concluded that they perished. Unfortunately, Walford did not enjoy our advantage of subsequent studies in the Bight to evaluate the fate of westward-drifting larvae. In contrast, Colton and Temple (1961) found 0-group haddock abundant west of Nantucket Shoals in two years, 1948 and 1950. Because the 1948 and 1950 year classes represented the two strongest since the compilation of statistics began in 1928, and because older haddock seldom occurred west of Nantucket Shoals, they too concluded that the young fish migrated back to Georges Bank.

Our results support previous suggestions that knowledge about the transport of spawning products is important for understanding the processes which determine year class strength (Harden Jones 1968; Bailey 1981; Parrish et al. 1981). The mass transport of larvae off Georges Bank in 1987 demonstrates that advective processes can result in almost complete removal of the spawning products from their normal habitat. This result, combined with the fact that in three other years in the 27-yr bottom trawl time series, >50% of the recently recruited 0-group haddock were located in the Middle Atlantic Bight, suggests that the transport of larvae off the Bank occurs with sufficient frequency and magnitude to be an important factor in the recruitment dynamics of this stock. However, if our conclusion that young haddock from the Middle Atlantic Bight migrated back to Georges Bank is accepted, large-scale errant drift does not necessarily result in year class failure. For the 1987 haddock year class, the question of whether overall recruitment in the fall of 1988 would have been greater or less in the absence of the large-scale transport to the Middle Atlantic Bight is critical and, in general, the importance of errant drift needs to be evaluated not only in terms of its magnitude and frequency but also in relation to the resulting survival and return rates.

Acknowledgements

The authors wish to thank their many co-workers who spent numerous days at sea and hours in the laboratory to collect and process the samples upon which this report is based.

References

AZAROVITZ, T. 1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. Can. Spec. Publ. Fish. Aquat. Sci. 58: 62–67.

BAILEY, K. 1981. Larval transport and recruitment of Pacific hake, *Merluccius productus*. Mar. Ecol. Prog. Ser. 6: 1–9.

BOLZ, G., AND R. LOUGH. 1988. Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments. Fish. Bull. U.S. 86(2): 223–236.

BOWMAN, R. 1981. Food of 10 species of Northwest Atlantic juvenile groundfish. Fish. Bull. U.S. 79(1): 200–206.

BUMPUS, D. 1976. Review of the physical oceanography of Georges Bank. Int. Comm. Northwest Atl. Fish. Res. Bull. 12: 119–134.

BUTMAN, B., J. LODER, AND R. D. BEARDSLEY. 1987. The seasonal mean circulation: observations and theory, Chap. 11, p. 125–138. *In* R. Backus and D. Borne [ed.] Georges Bank. The MIT Press, Cambridge, MA 593 p.

CHASE, J. 1955. Winds and temperature in relation to the brood strength of Georges Bank haddock. J. Cons. 21: 17–24.

CLARK, S., W. OVERHOLTZ, AND R. HENNEMEUTH. 1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northwest Atl. Fish. Sci. 3: 1–27.

COHEN, E., D. MOUNTAIN, AND W. SMITH. 1983. Physical processes and year class strength of silver hake and haddock on Georges Bank. NEFC, Woods Hole, MA, Lab Ref. No. 83-06: 18 p.

COLTON, J. JR., AND R. TEMPLE. 1961. The enigma of Georges Bank spawning. Limnol. Oceanogr. 6: 280–291.

ENVIRONMENTAL PROCESS DIVISION. 1988. Plan for study-response of the habitat and biota of the inner New York Bight to abatement of sewage sludge dumping. NOAA Tech. Memo. NMFS F/NEC-55: 34 p.

1992. Response of the habitat and biota of the inner New York Bight to abatement of sewage sludge dumping. Third Annual Progress Report 1989. NOAA Tech. Memo. NMFS F/NEC. (In press)

FREEDLAND, G., AND D. SWIFT. 1978. Surficial sediments: MESA New York Bight Monogr. 10, New York Sea Grant Institute, Albany, NY. 93 p.

GRAVARIS, S. 1988. Assessment of haddock in NAFO Division 5Z. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 88/64: 36 p.

GROSSLEIN, M. 1969. Groundfish survey program of BCF Woods Hole. Comm Fish. Rev. 31: 22–35.

HARDEN JONES, J. 1968. Fish migration. Arnold Press, London.

HARDY, J. JR. 1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval and juvenile stages. Vol. II. U.S. Dep. Inter. Biol. Serv Prog. FWS/OBS-78/12.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 20: 1–228.

HOLZWARTH, T., AND D. MOUNTAIN. 1990. Surface and bottom temperature distributions from the Northeast Fisheries Center spring and fall bottom trawl survey program, 1963–1987. NMFS Northeast Fisheries Center, Woods Hole, MA, Ref. Doc. 90-03.

LAURENCE, G., AND C. ROGERS. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus*(L.)). J. Cons. 36(3): 220–228.

LOUGH, R., AND G. BOLZ. 1989. The movement of cod and haddock larvae onto the shoals of Georges Bank. J. Fish. Biol. 35(Suppl. A): 71–79.

LOUGH, R., P. VALENTINE, D. POTTER, P. AUDITORE, G. BOLZ, J. NELSON, AND R. PERRY. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Mar. Ecol. Prog. Ser. 56: 1–12.

MANNING, J., AND L. LIERHEIMER. 1988. Description of the 1987 oceanographic conditions on the northeast continental shelf. NMFS Northeast Fisheries Center, Woods Hole, MA, Ref. Doc. 88-01.

MILLER, D., J. COLTON, JR., AND R. MARAK. 1963. A study of the vertical distribution of haddock larvae. J. Cons. 28: 37–49.

MORSE, W. 1984. An assessment of the Georges Bank haddock stock based on larvae collected on MARMAP plankton surveys, 1977–1982, p. 67–82. *In* P. Berrien, W. Morse, and M. Pennington [ed.] Recent estimates of adult spawning stock biomass off the northeastern United States from MARMAP ichthyoplankton surveys. NOAA Tech. Mem. NMFS-F/NEC-30: 111 p.

MOUNTAIN, D. 1989. TEMPEST: a computer program for estimating temperature on the northeast continental shelf. NEFC Ref. Doc. 89-02.

1991. The volume of shelf water in the Middle Atlantic Bight: seasonal and interannual variability, 1977–1987. Cont. Shelf Res. 11(3): 251–267.

MOUNTAIN, D., AND T. HOLZWARTH. 1990. Surface and bottom temperature distributions for the northeast continental shelf. NOAA Tech. Memo. NMFS-F/NEC-73.

MOUNTAIN, D., AND R. SCHLITZ. 1987. Some biologic implications of the circulation, p. 392–394. *In* R. Backus and D. Borne [ed.] Georges Bank. The MIT Press, Cambridge, MA. 593 p.

OVERHOLTZ, W., S. CLARK, AND D. WHITE. 1983. A review of the status of the Georges Bank and Gulf of Maine haddock stocks for 1983. NMFS, NEFC, Woods Hole Lab. Ref. Doc. 83-23.

PARRISH, R., C. NELSON, AND A. BAKUN. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1(2): 175–203.

SERCHUK, F., AND R. SMOLOWITZ. 1980. Size selection of sea scallops by an offshore survey dredge. ICES C.M. Doc. No. K:24: 38 p.

SHERMAN, K. 1980. MARMAP, a fisheries ecosystem study in the Northwest Atlantic: fluctuations in ichthyoplankton–zooplankton components and their potential for impact on the system, p. 9–37. *In* Diemer, F. F. Vernberg, and D. Mirkes [ed.] Advanced concepts in ocean measurements for marine biology. Belle Baruch Inst. for Mar. Biol. and Coastal Res. University of South Carolina Press, Columbia, SC.

SHERMAN, K., W. SMITH, W. MORSE, M. BERMAN, J. GREEN, AND L. EJSYMONT. 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18: 1–19.

SIBUNKA, J., AND M. SILVERMAN. 1984. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina to Cape Sable, Nova Scotia (1975–1983). Atlas No. 1. Summary of operations. NOAA Tech. Memo. NMFS-F/NEC-33: 306 p.

1989. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina to Cape Sable, Nova Scotia (1984–1987). Atlas No. 3. Summary of operations. NOAA Tech. Memo. NMFS-F/NEC-68: 197 p.

SMITH, W., AND W. MORSE. 1985. Retention of larval haddock, *Melanogrammus aeglefinus*, in the Georges Bank region, a gyre-influenced spawning area. Mar. Ecol. Prog. Ser. 24: 1–13.

SURVEY WORKING GROUP, NEFC. 1988. An evaluation of the bottom trawl survey program of the Northeast Fisheries Center. NOAA Tech. Memo. NMFS-F/NEC-52.

WALFORD, L. 1938. Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. Fish. Bull. U.S. 49: 1–73.

Rent Capture in an Individual Transferable Quota Fishery

R. Quentin Grafton

Economics Department, University of British Columbia, Vancouver, B.C. V6T 1Y2, Canada

Grafton, R. Q. 1992. Rent capture in an individual transferable quota fishery. Can. J. Fish. Aquat. Sci. 49: 497–503.

The problem of capturing economic rent in a fishery regulated by an individual transferable quota scheme is addressed using a profit tax and a quota tax as two methods of rent collection. Using a theoretical model of a fishery with representative fishers employing different harvesting functions, the effects of the taxes are evaluated with respect to their ability to capture rent, flexibility to adjust to changes in the fishery, effects upon economic efficiency, the burden of taxation on different fishers, and ease of implementation. A quota tax is shown to be preferred over a comparable profit tax by those fishers who earn the highest average net returns on quota owned. A quota tax also has the potential to allow fishers to capture the full benefits of efficiency improvements. The profit tax can allow for greater risk sharing between the regulator and fishers and is able to capture the entire rent in the fishery in both the short and long run.

L'auteur examine le problème du recouvrement d'une rente économique dans le cas d'une pêche faisant l'objet d'un régime de contingents individuels transférables, par l'entremise d'impôts sur bénéfices et sur contingents. À l'aide d'un modèle théorique d'une pêche effectuée par des pêcheurs représentatifs utilisant différentes méthodes de capture, il évalue les incidences de tels impôts pour ce qui est de leur capacité de recouvrement d'une rente, la souplesse d'ajustement à des variations de la pêche, les incidences sur l'efficience économique, le fardeau fiscal pour les divers pêcheurs et la facilité d'application. Il montre qu'un régime d'impôts sur les contingents est préférable à un régime semblable d'impôts sur bénéfices dans le cas de pêcheurs qui obtiennent le rendement net moyen le plus élevé sur leurs contingents. De plus, un régime d'impôts sur contingents peut permettre aux pêcheurs de tirer le plein avantage d'améliorations de l'efficacité. De son côté, le régime d'impôts sur bénéfices peut permettre un plus grand partage des risques entre les organismes de réglementation et les pêcheurs et de recouvrer en totalité la rente, tant à court terme qu'à long terme.

Received February 12, 1991
Accepted October 10, 1991
(JA895)

Reçu le 12 février 1991
Accepté le 10 octobre 1991

Economic rent may be defined as the payment in excess of the minimum required to bring into production an input or factor of production that is fixed in supply. For nonrenewable resources such as minerals, several methods of capturing rent exist, including a resource rental tax, profit, sales, and capital gains taxes, and royalty payments at some proportion of the estimated total value of the resource. In the forestry industry, resource users are often charged a royalty on the volume of trees logged. In contrast, in fisheries, there is a general failure by regulators to prevent rent dissipation or an attempt to capture rent where it may exist. One explanation for this phenomenon is that social objectives such as employment maximisation dominate economic efficiency in the management of fishery resources. Notwithstanding these objectives, an important question to be addressed is what are the preferred method(s) for the capture of economic rent from a fishery?

In an open access fishery where there is a divergence between private and social costs, total fishing effort tends to exceed the level that maximises the net returns in the fishery. In regulated fisheries, this externality or divergence between private and social costs may continue to exist where there are controls on the total harvest but there are ineffective restrictions upon fishing effort. In such fisheries, the incentive remains for fishers to compete for the limited harvests leading to excess effort and capacity above that necessary to harvest the total allowable catch (TAC). The result in both cases is the dissipation of potential rents (Munro and Scott 1985, p. 657–664).

One management system that attempts to improve economic efficiency and reduce the externality problem is an individual quota management scheme. In a quota-managed fishery, the resource owner determines a desired TAC which is then allocated among fishers in the form of harvesting rights. Individual quotas provide fishers with a greater assurance of catching their respective shares of the harvest. In turn, this may reduce racing behaviour between fishers to "catch the fish before someone else does" and allow quota holders to harvest the resource in a more efficient manner. Net returns in the fishery may be further enhanced by allowing transferability of quota so that more efficient operators can acquire a greater share of the total harvest. By setting a TAC in a quota management system such that harvesting rights are scarce, the resource owner can allow for the existence of economic rent. Theoretically, this potential rent may then be captured by taxes and/or fees on quota with no loss in efficiency (see Ghatak and Ingersent 1984, p. 123–124, for definitions of allocative, technical, and economic efficiency).

Quota management systems have been implemented in Atlantic Canada's offshore fishery (Fraser and Jones 1989; Gardner 1989), in the Icelandic fisheries (Arnason 1986), in some of the commercial fisheries of the Great Lakes, Australia's southern bluefin tuna fishery (Geen and Nayar 1989), and in most of the coastal and offshore fisheries of New Zealand (Clark et al. 1989). The characteristics of these schemes vary according to the objectives of the resource owner and the nature of the fisheries. This paper evaluates two rent capture methods for a particular individual transferable quota (ITQ) scheme where quota is denominated in quantities of fish, is fully transferable, and provides the holder with a harvesting right in perpetuity. A stylised fishery model with numerical results is presented as an aid in the analysis.

The Model

The theoretical environment assumed for evaluating alternative methods of rent caputre is that of a fishery where management is vested in a regulator. In place in the fishery is an individual quota management scheme, where quota was originally allocated *gratis* to fishers, trades at a positive price, and is denominated in quantity of fish that may be harvested per unit of time. Initially operating in the fishery are two types of fishers each maximising economic profits over time in a deterministic environment and who differ only with respect to their fixed costs of production and harvesting technology.

The model assumes a steady-state fishery where the total harvest equals the growth in the biomass in every period. This assumption is applied *not* because population dynamics and uncertainty (Clark 1985, p. 210–258) or the optimal approach path to a steady state (Clark and Munro 1982, p. 31–54) are considered unimportant, but rather to focus attention on the issue of rent capture in the most simple framework possible.

In the first instance, it is useful to examine the optimum harvest, number of fishers, the technology employed, and the total rent *if* the regulator had complete control over the fishery and maximised the present value of the resource rent. In this first best or long-run situation, the regulator seeks to maximise the present value of the sum of individual fisher profits. In the regulator's problem, profits are defined as the total revenue of fishers less fixed and variable costs.

The notation used to describe the problem is defined as follows:

Π is the total fishery rent
k denotes individual fisher employing the F1 technology
j denotes individual fisher employing the F2 technology
N is the optimum number of F1 type fishers
M is the optimum number of F2 type fishers
P is the exogenous price of fish
C is the exogenous cost per unit of fishing effort
$FC1$ is the fixed cost of a F1 type fisher
$FC2$ is the fixed costs of a F2 type fisher
q_{1k} is the harvest of an individual k, F1 type fisher
e_{1k} is the fishing effort of an individual k, F1 type fisher
q_{2j} is the harvest of individual j, F2 type fisher
e_{2j} is the fishing effort of an individual j, F2 type fisher
b is the total fish biomass
$\bar{b}$ is the maximum attainable biomass
B is a constant.

Regulator's Problem

Maximise with respect to $[N, M, b, e_{1k}, e_{2j}]$:

$$\Pi = \sum_{k=1}^{N} [Pq_{1k} - Ce_{1k} - FC1] + \sum_{j=1}^{M} [Pq_{2j} - Ce_{2j} - FC2]$$

subject to

$$(1) \quad q_{1k} = 2e_{1k}^{1/2}\, b$$

$$(2) \quad q_{2j} = e_{2j}^{1/2}\, b$$

$$(3) \quad \sum_{k=1}^{N} q_{1k} + \sum_{j=1}^{M} q_{2j} = Bb(\bar{b} - b)$$

where equation (1) is the harvest function from employing technology one, equation (2) is the harvest function from employing technology two and equation (3) is an equilibrium condition that ensures that the total harvest equals the growth in the biomass.

In this model, the harvest functions are increasing and concave with respect to effort where effort is defined as some composite variable of a fisher's inputs. Concavity of the harvesting function is defined by (4) with strict concavity defined by a strict inequality:

$$(4) \quad \frac{\partial^2 q(e;\, b)}{\partial e^2} \leqslant 0 \ \forall e$$

where $q(e;\, b)$ is the harvest function, e is the fishing effort, and b is the total fish biomass.

Concavity of the harvesting function may arise from gear saturation that reduces the catchability of fishing gear and congestion among fishing vessels on fishing grounds (Clark 1990, p. 222–225). The harvest is increasing with respect to the biomass of the fishery indicating, *ceteris paribus*, that a greater stock of fish will yield a higher catch per unit of effort. The growth function of the fishery assumes a parabolic relationship between surplus production or yield and the size of the stock. This is derived from the assumption that a fish stock produces its greatest harvestable surplus when it is at an intermediate and *not* at a maximum level of abundance. This may be due to several causes including the fact that recruitment of new year classes into a fishery is often hampered by higher densities and that greater pressure on food stocks often means a larger fraction of calories is used merely to maintain life rather than for growth (Ricker 1987, p. 309–316).

The solution to the problem will depend on the values of the exogenous variables P, C, B, $\bar{b}$, $FC1$, and $FC2$. Under the assumption of a deterministic environment and that the growth in the biomass equals the total harvest in every period, the solution to the regulator's problem will also maximise the present value of rents in the fishery.

As fisheries are rarely at a long-run optimum, it is useful to compare the solution to the regulator's problem with the short-run equilibrium in an ITQ fishery, the short run being defined as the time necessary to allow for transactions of quota among fishers already in the fishery and the long run as the time necessary to allow for entry and exit of all vessels. In making the comparison, it is assumed that the initial number of vessels fishing and the TAC for the ITQ fishery are the same as in the long-run equilibrium. This TAC is further assumed to be divided by the regulator among all fishers at no charge upon the introduction of the ITQ management. Operating in the fishery are two types of fishers: those who employ a type-one technology (F1) and those who employ a type-two technology (F2). The F1 type fishers are assumed to have a higher catchability coefficient but higher fixed costs than the F2 type fishers.

In the ITQ fishery, it is assumed that each fisher buys/sells or leases the quota they desire immediately after receiving their initial allocation of quota until a market equilibrium is achieved. Each fisher is assumed to maximise economic profits over time by choice of fishing effort and the quantity traded and behave as if he is able to lease all his quota at the price at which it last traded multiplied by the competitive rate of interest. The economic profit of fishers is defined as their total revenue less fixed and variable harvesting costs and less the opportunity cost of owning quota at each time period. A fisher's opportunity cost is defined as the annuity that would be earned if quota were sold and the funds invested elsewhere in the economy at a competitive rate of interest. It is best understood in the context that quota is an asset and imposes a cost on its owner whether it is bought, leased, or obtained *gratis* from the regulator.

The maximisation problem faced by fishers at the beginning of period $t = 1$ when quota is first traded is presented below.

The notation used to describe the problem is as defined previously and includes the following:

r is the competitive rate of interest
e_{kt} is fishing effort in period t by fisher k
e_{jt} is fishing effort in period t by fisher j
Γ is the market price of quota
$A_{k,j}$ is the initial quota allocation to fisher k, j
$w_{k,j}$ is the quantity traded by fisher k, j which is positive if quota is bought/leased and negative if sold/rented out.

Maximisation Problem of Fishers

Fisher k employing an F1 type technology maximises with respect to $[e_{kt}, w_k]$:

$$\sum_{t=1}^{\infty} \frac{1}{(1+r)^t}[Pq_{1k}(e_{kt}; b) - Ce_{kt} - FC1 - \Gamma r(A_k + w_k)]$$

subject to

$$(5) \quad q_{1k}(e_{kt};b) \leq A_k + w_k.$$

Fisher j employing an F2 type technology maximises with respect to $[e_{jt}, w_j]$:

$$\sum_{t=1}^{\infty} \frac{1}{(1+r)^t}[Pq_{2j}(e_{jt}; b) - Ce_{jt} - FC2 - \Gamma r(A_j + w_j)]$$

subject to

$$(6) \quad q_{2j}(e_{jt}; b) \leq A_j + w_j.$$

The short-run quota equilibrium for quota is solved by deriving the individual quota demands of the two types of fishers and setting the sum of the demands equal to the TAC. The market price of quota is determined from the equilibrium condition which if substituted into the respective quota demands can solve for the post-trade quota distribution. This equilibrium represents the quota distribution that would arise given the initial conditions in the fishery. In general, this short-run equilibrium will differ from the long-run optimum because it does not account for the possibility of entry of additional vessels into the fishery.

In solving for the short-run equilibrium, note that if quota is valuable, then the optimal harvest of a fisher will never be less than the quota owned in a deterministic environment. Consequently, (5) and (6) hold with strict equality such that $A_{k,j}$ and $w_{k,j}$ can be substituted by $q_{1k,2j}$ in the respective maximisation problem. Using the fishers' harvesting functions one may also solve for the level of effort (e_{kt}, e_{jt}) as a function of the quantity harvested and the biomass.

In a deterministic environment the maximisation problem faced by an F1 type fisher, therefore, simplifies to

$$H1 = \frac{1}{r}\left[Pq_{1k} - C\frac{q_{1k}^2}{4b^2} - FC1 - \Gamma q_{1k}r\right].$$

Maximising with respect to q_{1k} the following first-order condition is obtained:

$$(7) \quad \frac{\partial H1}{\partial q_{1k}} = \frac{1}{r}\left[P - \frac{Cq_{1k}}{2b^2}\right] - \Gamma = 0.$$

Solving (7) in terms of q_{1k}, we obtain

$$(8) \quad q_{1k}^* = \frac{2b^2}{C}[P - \Gamma r].$$

The maximisation problem faced by an F2 type fisher simplifies as

$$H2 = \frac{1}{r}\left[Pq_{2j} - C\frac{q_{2j}^2}{b^2} - FC2 - \Gamma q_{2j}r\right].$$

Maximising with respect to q_{2j} the following first-order condition is obtained:

$$(9) \quad \frac{\partial H2}{\partial q_{2j}} = \frac{1}{r}\left[P - \frac{2Cq_{2j}}{b^2}\right] - \Gamma = 0.$$

Solving (9) in terms of q_{2j}, we obtain

$$(10) \quad q_{2j}^* = \frac{b^2}{2C}[P - \Gamma r].$$

The short-run equilibrium price is found by equating the quota allocated to the sum of the individual demands for quota. Defining X and Y, respectively, as the number of F1 and F2 type fishers initially allocated quota and the TAC as the total quota allocation, the following short-run equilibrium condition is obtained:

$$(11) \quad \text{TAC} = \frac{2Xb^2}{C}[P - \Gamma r] + \frac{Yb^2}{2C}[P - \Gamma r].$$

Solving (11) in terms of the market price of quota (Γ), we obtain

$$(12) \quad \Gamma = \frac{P}{r} - \frac{2C[\text{TAC}]}{[4X + Y]rb^2}.$$

At the short-run equilibrium, no further trades will take place until there is entry of new vessels into the fishery. This is because the marginal value of quota to F1 and F2 type fishers currently in the fishery is identical and equal to the market price. Differentiating (12), the short-run quota price is found to be increasing with respect to the price of fish, the number of fishers, and the biomass and decreasing with respect to the cost per unit of effort, the interest rate, and the initial quota allocation.

To compare the return of fishers and to assess the distributional impacts of different methods of rent capture, it is useful to present a numerical example. This example does not purport to be representative of an actual fishery and is provided only for illustrative purposes. The following values are assumed for the exogenous variables: $P = 2$, $C = 3.2$, $r = 0.1$, $B = 10$, $\bar{b} = 20$, and $FC1 = 80$, $FC2 = 40$. The optimum harvest and the type and number of fishers employed in the long-run optimum can be derived by solving an algorithm that maximises the sum of individual profits at each biomass level for different number of fishers of the two types. The global optimum is found by searching for the highest total profits over all biomass levels. The solution is to set $b^* = 14$, $N = 6$, $M = 0$, $q_{1k}^* = 140\ \forall k$, $q_{2j}^* = 0\ \forall j$, which yields a total rent per time period of 720 monetary units. The rent being the sum of the individual profits of fishers which is defined as total revenue less total fixed and variable harvesting costs. At the long-run optimum, the biomass is 14 and the total harvest is 840 units per time period which is caught by six F1 type fishers each harvesting 140 units. At an interest rate of 10%, this yields a capitalised rent from the fishery of 7200 monetary units.

By assumption, the quota-managed fishery sets a TAC equal to the long-run optimum of 840 quota units and allocates quota to the same number of fishers but equally among the two types of fishers. The amount allocated to individual fishers has no effect on the market equilibrium and ultimate distribution of quota, but does affect the cost/return to fishers from buying/selling or leasing quota. At the short-run equilibrium, each of the three F1 type fishers harvests 224 units, while each of the three F2 type fishers harvests 56 quota units. It is assumed that the 84 quota units that were obtained by the F1 type fishers are leased and not bought from the F2 fishers at an amount equal to the market price of quota multiplied by the rate of interest. At a market price of quota of some 1.71/unit and an interest rate of 10%, this represents an annual cost/return to each F1/F2 type fisher of some 14.4 monetary units. At the equilibrium and prior to entry of other vessels, the total annual rent available from the fishery in the short run is some 552 monetary units.

A comparison of the total rent in the fishery in the long run and the short run illustrates the importance of initial conditions for rent capture. Merely setting the TAC equal to the first best harvest level and allocating quota to the same number of fishers as in the long-run optimum is insufficient to ensure that the rent available in the short run will be the same. The short and long run will only coincide if there is instantaneous adjustment in quota *and* vessels or if the number and type of vessels in the long run is the same as that when quota are first allocated. For example, if the fishery at implementation of ITQ's had only six F1 type fishers, then the long-run optimum would arise immediately because there would be no adjustment time required for entry and exit of vessels.

Given the potential increase in welfare in moving from the short-run to the long-run equilibrium, one may expect the distribution of quota to change over time as some vessels are retired and others added to the fishery. Provided there are perfect markets and no barriers to entry, the long run is achievable in the time necessary to allow for the entry and exit of all vessels. Where, however, market imperfections exist such as capital constraints on fishers acquiring new vessels or buying quota, the long-run optimum may never arise. In such circumstances, the capture of rent by the regulator will reduce the cost of acquiring quota. In turn, this may help new entrants into the fishery and aid in the adjustment process to the long-run equilibrium.

Rent Capture Methods Compared

Given that the short-run equilibrium allows for the existence of both types of fishers and because regulators are as concerned about the short run as they are about the long run, the implications of rent capture methods are first addressed assuming the short-run quota distribution.

The two methods of rent capture examined are a quota tax based upon the price of quota and a profit tax based on fishers' individual profits. A form of a quota tax has been implemented in New Zealand's ITQ fisheries, while the profit tax is a common method of taxing individuals and enterprises. In New Zealand, resource rentals are set on an annual basis per quantity of quota and are payable in quarterly installments. The rental charges are determined on the basis of quota values, expected net returns of fishers, and other factors deemed important by the regulator.

TABLE 1. Annual net profits and rent captured under quota and profit tax schemes at the short-run equilibrium.

Scenario	Profit	Economic profit	Rent captured
Pretax			
F1	148.8	124.8	0
F2	35.2	25.6	0
Total	552	451.2	0
After-tax 100% quota			
F1	124.8	124.8	24
F2	11.2	11.2	24
Total	408	408	144
After-tax 75% quota			
F1	130.8	124.8	18
F2	17.2	14.8	18
Total	444	418.8	108
After-tax 26.09% profit			
F1	112.76	95.02	39.80
F2	23.24	16.15	8.20
Total	408	333.50	144
After-tax 19.57% profit			
F1	121.95	102.65	29.66
F2	26.05	18.33	6.34
Total	444	362.92	108

Before evaluating the effects of these taxes, it is useful to examine the profits and economic profits of fishers prior to rent capture (Table 1). Under the assumption that the earnings of fishers outside of the fishery are zero, the rent in the fishery is simply the sum of individual profits of the three fishers of each type.

Quota Tax

The quota tax proposed sets a tax at some proportion of the quota price multiplied by a competitive rate of interest, i.e.

$$\text{Rent captured} = t \times \Gamma \times r \times q$$

where t is the quota tax rate, Γ is the market price of quota before taxes are imposed, r is the competitive rate of interest, and q is number of quota units owned. A prerequisite for such a tax is a competitive quota market where prices are known by both the regulator and fishers.

The quota tax examined in this paper is assessed on the pretax quota price. A problem with this approach is that in an actual fishery the rent captured would not vary with changes in the expected value of the rent. If, however, a quota tax was assessed on the current quota price after announcement of rent capture, then the rent collected would reflect changes in the value of the rent. This is because the current quota price plus the expected rent captured per unit of quota would equal the value of quota without rent capture. Consequently, changes in the value of the expected rent would be reflected in the current quota price and hence in the rent collected. To capture the same amount of rent with both quota taxes, however, the tax rate applied to the current quota price would have to be greater than that applied to the prequota price. For example, a 100% tax rate assessed on the price of quota *after* announcement of rent capture and adjustment in the quota market would collect the same amount of rent as a 50% tax rate assessed on the pretax quota price.

We examine quota tax rates of 100 and 75% of the pretax quota price. A tax rate at *less* than 100%, however, is strongly recommended, as it would drive the quota price to zero. Such an outcome is not desirable because quota prices provide important information to fishery managers (Arnason 1989, p. 215). Under the 100 and 75% tax rates, both F1 and F2 fishers earn positive profits and economic profits (Table 1).

For the 100% quota tax, economic profits and profits are identical because the opportunity cost of owning quota is zero. Under the 75% tax rate, the economic profit of F1 type fishers is the same as that under the 100% tax rate. This is because with the lower tax rate, after-tax profits are increased by the amount of quota owned multiplied by one quarter of the lease price. Correspondingly, the opportunity cost of owning quota increases from zero to the amount that would be earned, after taxes, if the quota was leased to someone else. Given that the reduced tax paid with a 75% quota tax is exactly offset by the increase in the opportunity cost of owning quota, economic profits remain unchanged. For the F2 type fishers, economic profits do change with a different tax rate. This is because the reduction in tax is based upon the amount of quota owned, while the opportunity cost is calculated on the amount of quota that is *not* leased. In the case of the F2 type fishers, the amount of quota owned (140 quota units) exceeds the amount of quota used (56 quota units) such that economic profits rise with a reduction in the tax rate.

Under the 100% quota tax rate the regulator collects 144 monetary units of rent, while with a 75% tax rate, 108 monetary units are appropriated (Table 1). These amounts represent some 26 and 20% of the total rent in the fishery. The reason that even a 100% quota tax is unable to collect the entire rent in the short run is because the quota price reflects the marginal profit of an additional quota unit rather than the average profit per quota unit. Only when the two values coincide, as in the long run, is a quota tax capable of capturing the entire rent in the fishery.

The proposed 100% quota tax also has the distinguishing feature that it will always leave fishers who use all their quota themselves with nonnegative after-tax profits provided that such individuals exit a fishery whenever they face negative economic profits. For such fishers, their after-tax profits will exactly equal their pretax economic profits. Those fishers who only use a share of their quota may face positive or negative after-tax profits with a 100% quota tax depending upon the characteristics of the fishery.

Implementing a quota tax is complicated by the need to determine a "competitive rate of interest" and a market price of quota. In deciding upon the former, the regulator must avoid a rate that is too high such that more than rent is collected and setting a rate too low such that less rent than desired is captured. If a high priority is to avoid distortions from taxes, setting a rate equal to a risk-free rate of return may be desirable. In determining a quota price, it should be realised that prices can vary significantly over a fishing season and between bids (Linder et al. 1989). In such a situation, assessment of the tax on a quarterly basis with suitable adjustments and an allowance for tax deferral may be desirable.

Profit Tax

A profit tax captures rent at a fixed proportion of fisher profit and is applied prior to any standard company profit taxes, i.e.

$$\text{Rent captured} = t \times \theta_i$$

where t is the profit tax rate and θ_i is the pretax profit of fisher i.

To properly compare a profit and quota tax, the total rent captured in the two schemes must be the same. A profit tax at some 26 and 20% of fisher profits provides an equivalent comparison with the 100 and 75% quota taxes (Table 1).

Under both the quota and profit tax the distribution of quota is unchanged. However, comparison of the rent captured by the two taxes reveals important differences in the burden of taxation of the two schemes (Table 1). For example, all fishers pay 24 and 18 monetary units, respectively, under the 100 and 75% quota taxes. In contrast, F1 type fishers pay 39.8 and 29.66 monetary units and F2 type fishers pay 8.2 and 6.34, respectively, under the comparable profit taxes. The example illustrates the important result that fishers with a higher average profit per unit of quota owned (F1) will pay proportionately less rent to a regulator with a quota tax than an equivalent profit tax (see Appendix, proposition 1). It suggests that a quota tax would be favoured by fishers who through their technology or other factors earn higher than average net returns per quota unit.

In the example presented, it is assumed that quota is only leased on an annual basis and not purchased or sold. In an actual fishery, both types of transactions would occur. A consideration in any type of rent capture is to ensure that the purchase and lease prices of quota reflect future taxes to a regulator. If taxes are imposed unexpectedly after contracts are made for leasing quota, then the lessors are penalised because they receive a lower than expected return net of taxes. If taxes are imposed unexpectedly after quota is purchased, then the buyers of quota are penalised. In the latter case, fishers who have paid too high a price for quota may be unable to derive sufficient revenue after taxes to cover their capital costs. Such problems, however, may be avoided if the type and rate of rent capture to be applied in the fishery is announced simultaneously with the introduction of transferable quotas.

In addressing the issue of economic efficiency, if only economic rents are being captured then both taxes should be neutral. However, if economic profits are viewed as the incentive for innovation (Schumpeter 1961 (ca. 1934), p. 128–156), then a quota tax may be preferable. This is because an innovative fisher is potentially able to capture the full returns of any efficiency gains with a quota tax. Such profits accrued from individual innovation are not an economic rent attributable to the scarcity of the resource but are a function of the skills of the given fisher. Only when an innovation becomes widely diffused such that the gains from its use are reflected in the price of quota will a quota tax on the current price of quota capture a portion of these benefits.

Another difference between the rent capture schemes is that a profit tax shares risk between fishers and the regulator because returns are calculated *ex-post*, while a quota tax puts the full burden of risk on fishers because it is calculated on an *ex-ante* basis. For instance, in an ITQ-managed fishery, those operators incurring short-run losses with the expectation of positive profits in the future will not pay a resource rental with a profit tax but will do so with a quota tax. Such risk sharing may be desirable, as it may reduce the effect of adverse fluctuations on fishers. A quota tax may, however, be modified to allow for risk sharing over time if fishers earning negative returns can defer their taxes and pay them at a later date with interest.

A characteristic of both the profit and quota taxes is their flexibility to adjust to changes in factor prices and variations in the fecundity of fish stocks. A profit tax does this in accordance with fisher profits, while a quota tax can be devised to vary with changes in the current quota price. Operationally, a profit tax should be no more demanding on the regulator than a quota tax provided that structures exist for recording, auditing, and taxing businesses. Deductions from profits such as investment write-offs and accelerated depreciation, however, can give fishers a greater opportunity for tax avoidance. Implementing a profit tax in a multispecies fisheries also poses problems in apportioning costs if the regulator wishes to collect rent from only one species.

Discussion

An adequate comparison of the rent capture methods requires an examination of their effects in both the short and long run. Over time, as all vessels are able to enter and exit the fishery, the long-run optimum is achieved. Given no barriers to entry and assuming that firms are earning normal profits outside the fishery, the cost of purchasing/leasing quota by new entrants would be such that they would earn zero profits. If this was not the case, the price of quota would rise to reflect the fact that new entrants could still earn positive profits from purchasing quota at the existing price.

At the long-run equilibrium, the average cost of fishers is at a minimum such that given exogenous prices the marginal profit of an addditional unit of quota is equal to the average profit per quota unit. As a result, the quota price without rent capture would equal the average profit per unit of quota. In this case, a quota tax equal to the price of quota without rent capture would collect the entire rent in the fishery. In general, this is not true in the short run and contrasts with a profit tax which is theoretically able to collect the entire rent in both the short and long run.

A useful comparison for any tax scheme in natural resources is of the revenue earned with that available from a once and for all auction of the property rights. Given perfect information, competitive bidding, and a discount rate by bidders equal to the social opportunity cost of capital for investments of comparable risk, an auction is theoretically able to return to the owner the maximum value of a resource (Heaps and Helliwell 1985, p. 427–430). If fishers who enter the fishery at a later data also participate in the auction, then the maximum potential rent can be appropriated by the regulator. If, however, fishers do not purchase quota until ready to use it, then a once and for all auction would return to the regulator only the maximum rent available from the fishery in the short run.

An alternative to a once and for all auction is an auction of quota for a time-limited tenure. Under such a system, the regulator is able to capture rent in both the short and long run. A difficulty with such an auction, however, is the uncertainty it may create for the quota user. Such uncertainty may impact negatively on the long-term investment in the fishery.

Conclusions

In general, the short- and long-run outcomes in a quota-managed fishery will differ whenever there is not an instantaneous adjustment in both quotas and vessels. The difference in the two outcomes and the adjustment time to reach the long-run equilibrium will depend upon the initial conditions in the fishery when ITQ's are first introduced. The initial conditions in the fishery are also important in the choice of a rent capture scheme and will affect the present value of rents captured by the regulator.

The quota tax has the potential of allowing fishers to capture the full benefits of efficiency improvements and may provide less opportunity for tax avoidance than a profit tax. For those fishers who harvest an amount equal to the quantity of quota they evaluate with an opportunity cost, their economic profits are also unchanged with a quota tax at any tax rate. On the basis of taxes paid, a quota tax will also be preferred over an equivalent profit tax by those fishers who earn the highest average net returns on the quota they own.

The profit tax has the advantage of allowing greater risk sharing between the regulator and fishers and its theoretically able to capture all rents in a fishery in both the short and long run irrespective of the harvesting functions of fishers.

Examining the taxes in the long run, it is notable that both a quota and profit tax can capture the total rent in the fishery at the long-run equilibrium. In comparison, a once and for all auction of quota can capture the total potential rent in the fishery provided that fishers who enter the fishery at a later date participate in the auction. If, however, fishers only purchase quota when they are able to fish, an auction will only capture the maximum available rent from the fishery in the short run.

Acknowledgments

The author greatly appreciates the helpful comments of Ragnar Arnason of the University of Iceland, Paul Bradley, Hisafumi Kusuda, Gordon Munro, Phil Neher, Harry Nelson, Bill Schworm, Margaret Slade, and Casey Van Kooten of the University of British Columbia, and anonymous referees in the preparation of this paper. The author remains fully responsible for all errors, omissions, and inconsistencies.

References

ARNASON, R. 1986. Management of the Icelandic demersal fisheries, p. 83–101. *In* N. Mollett [ed.] Fishery access control programs worldwide. Alaska Sea Grant Report No. 86-4, University of Alaska, Fairbanks, AK.

1989. Minimum information management with the help of catch quotas, p. 215–241. *In* P. A. Neher, R. Arnason, and N. Mollett [ed.] Rights based fishing. Kluwer Academic Publishers, Dordrecht, The Netherlands.

CLARK, C. W. 1985. Bioeconomic modelling and fisheries management. John Wiley and Sons, Toronto, Ont. 291 p.

1990. Mathematical bioeconomics: the optimal management of renewable resources. 2nd ed. John Wiley and Sons, Inc., New York, NY. 386 p.

CLARK, C. W., AND G. R. MUNRO. 1982. The economics of fishing and modern capital theory: a simplified approach, p. 31–54. *In* L. J. Mirman and D. F. Spulber [ed.] Essays in the economics of renewable resources. North-Holland, Amsterdam, The Netherlands.

CLARK, I., P. J. MAJOR, AND N. MOLLETT. 1989. Development and implementation of New Zealand's ITQ management system. Mar. Resour. Econ. 5(4): 325–350.

FRASER, C. A., AND J. B. JONES. 1989. Enterprise allocations: the Atlantic Canada experience, p. 267–288. *In* P. A. Neher, R. Arnason, and N. Mollett [ed.] Rights based fishing. Kluwer Academic Publishers, Dordrecht, The Netherlands.

GARDNER, M. 1989. Enterprise allocation system in the offshore groundfish sector in Atlantic Canada. Mar. Resour. Econ. 5(4): 389–414.

GEEN, G., AND M. NAYAR. 1989. Individual transferable quotas in the southern bluefin tuna fishery: an economic appraisal. Mar. Resour. Econ. 5(4): 365–388.

GHATAK, S., AND K. INGERSENT. 1984. Agriculture and economic development. The John Hopkins University Press, Baltimore, MD. 380 p.

HEAPS, T., AND J. F. HELLIWELL. 1985. The taxation of natural resources, p. 421–472. *In* A. J. Auerbach and M. Feldstein [ed.] Handbook of public economics. Vol. 1. North-Holland, Amsterdam, The Netherlands.

LINDER, R. K., H. F. CAMPBELL, AND G. F. BEVIN. 1989. Pricing the New Zealand fish stock under a quota management system. Department of Agricultural Economics Discussion Paper 4/89, University of Western Australia, Perth. 42 p.

MUNRO, G. R., AND A. D. SCOTT. 1985. The economics of fisheries management, p. 623–676. *In* A. V. Kneese and J. L. Sweeny [ed.] Handbook of natural resource and energy economics. Vol. 2. North-Holland, Amsterdam, The Netherlands.

RICKER, W. E. 1987. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SCHUMPETER, J. A. 1961 (ca. 1934). The theory of economic development. Translated by R. Opie. Oxford University Press, New York, NY. 255 p.

Appendix: Proof of Proposition 1

A fisher who earns a higher average profit per unit of quota owned will pay proportionately less rent to a regulator with a quota tax than with an equivalent profit tax in comparison with a fisher with a lower average profit per unit of quota owned. Similarly, a fisher with a lower average profit per unit of quota owned will pay proportionately more with a quota tax than with an equivalent profit tax relative to a fisher with a higher average profit per unit of quota owned.

Defining fisher *i*'s pretax profits as

$$\text{(A.1)}\quad \text{Pretax profit } \theta_i = Pq_i - C_i(q_i) - FC_i - \Gamma r w_i$$

where P is the exogenous price of fish, q_i is the harvest of fisher i, $C_i(q_i)$ is the variable cost function of fisher i, FC_i is the fixed cost of production fisher i, Γ is the price of quota, r is the competitive rate of interest, and w_i is the quantity of quota leased or rented out by fisher i.

The annual rent paid by fisher i with a profit tax at a rate t is

$$\text{(A.2)}\quad \text{Rent paid with profit tax} = t \times \theta_i.$$

The annual rent paid by fisher i with a quota tax at a rate α is

$$\text{(A.3)}\quad \text{Rent paid with quota tax} = \alpha \times \Gamma \times r \times (q_i - w_i).$$

Noting that the quantity of quota traded (w_i) equals the amount of quota used (q_i) less the amount initially allocated, then the first-order condition of fisher i is

$$\text{(A.4)}\quad \Gamma r = P - C_i'(q_i),\ \forall i$$

which holds for all fishers at the quota equilibrium if they face the same prices and interest rate.

Rewriting (3) in terms of (4):

$$\text{(A.5)}\quad \text{Rent paid with quota tax} = \alpha\,(P - C_i'(q_i))(q_i - w_i).$$

To ensure that a profit and quota tax capture the same amount of rent, the following condition holds:

$$\text{(A.6)}\quad t\left[\sum_{i=1}^{N} \theta_i\right] = \alpha\left[\sum_{i=1}^{N} (P - C_i'(q_i))(q_i - w_i)\right]$$

where N is the number of fishers.

Assuming average profit per quota unit owned satisfies

$$\text{(A.7)}\quad \frac{\theta_1}{q_1 - w_1} > \frac{\theta_2}{q_2 - w_2} > \cdots > \frac{\theta_N}{q_N - w_N}.$$

It can be shown that given (7):

$$\text{(A.8)}\quad \frac{t\theta_1}{\alpha(q_1 - w_1)(P - C_1'(q_1))} > \cdots > \frac{t\theta_N}{\alpha(q_N - w_N)(P - C_N'(q_N))}$$

where the numerator is the rental payment with a profit tax and the denominator is the rental payment with a quota tax which collectively satisfy condition (6).

Multiplying (7) by t/α, we obtain

$$\text{(A.9)}\quad \frac{t\theta_1}{\alpha(q_1 - w_1)} > \cdots > \frac{t\theta_N}{\alpha(q_N - w_N)}.$$

From (4) we note

$$\text{(A.10)}\quad \frac{1}{P - C_i'(q_i)} = \frac{1}{P - C_j'(q_j)},\ \forall i, j$$

such that multiplying (9) by (10):

$$\frac{t\theta_1}{\alpha(q_1 - w_1)(P - C_1'(q_1))} > \cdots > \frac{t\theta_N}{\alpha(q_N - w_N)(P - C_N'(q_N))}.$$

Grazers and Nutrients Simultaneously Limit Lotic Primary Productivity[1]

Walter R. Hill,[2] Harry L. Boston, and Alan D. Steinman

Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, TN 37831-6351, USA

Hill, W. R., H. L. Boston, and A. D. Steinman. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. Can. J. Fish. Aquat. Sci. 49: 504–512.

Nitrate and phosphate were added to two of four flow through channels in a second-order stream in eastern Tennessee to raise nutrient concentrations to 3–4 times background, while two of four sets of colonized ceramic tiles in each channel were raised above the substratum to exclude grazing snails (*Elimia clavaeformis*). Snail grazing maintained a thin layer of periphyton dominated by *Stigeoclonium* basal cells, regardless of nutrient regime. Although nutrient effects on periphyton ash-free dry mass were statistically insignificant, nutrient additions significantly increased chlorophyll a, especially where snails were excluded. Snail densities were 89% higher in nutrient-enriched channels. Photosynthesis–irradiance data suggested that nutrient enrichment increased self-shading in the periphyton. Areal-specific productivity was simultaneously limited by grazing and low nutrient concentrations: snail exclusion and nutrient enrichment both increased productivity >2 times. The negative effect of snails on areal-specific productivity was due to (1) reduction in biomass by cropping and (2) depression of chlorophyll-specific productivity. The means by which *Elimia* depresses chlorophyll-specific productivity is unclear, but the depression is clearly disadvantageous to food-limited grazers. Because *Elimia* was the dominant invertebrate, our results indicate that low nutrient concentrations limit secondary as well as primary production in autumn.

Du nitrate et du phosphate ont été ajoutés à deux des quatre chenaux d'un cours d'eau de second ordre de l'est du Tennessee afin d'élever les concentrations de bioéléments par un facteur de 3 à 4 fois la concentration ambiante, tandis que deux des quatre séries de carreaux céramiques colonisés placés dans chaque chenal ont été élevés au–dessus du substrat pour en exclure l'escargot brouteur *Elimia clavaeformis*. Indépendamment du régime nutritif, le broutage n'a pas éliminé la mince couche de périphyton où dominait des cellules basales de *Stigeoclonium*. Même si les incidences de bioéléments sur la masse sèche sans cendre du périphyton n'étaient pas statistiquement significatives, l'ajout de bioéléments a entraîné une augmentation significative de la chlorophylle a, surtout en l'absence d'escargots. Par contre, la densité des escargots étaient de 89% plus élevée dans les chenaux enrichis. Les données sur la photosynthèse et le niveau d'éclairement portent à croire que l'ajout de bioéléments a mené à une augmentation de l'auto-ombrage du périphyton. Par contre, la productivité spatiale était simultanément limitée par le broutage et de faibles concentrations de bioéléments; l'élimination des escargots et l'ajout de bioéléments ont tous deux mené à une augmentation de la productivité par un facteur supérieur à 2. L'incidence négative des escargots sur la productivité spatiale résultait des deux facteurs suivants : 1) la réduction de la biomasse par le broutage et 2) la baisse de la productivité liée à la chlorophylle. On ne sait pas de quelle manière *Elimia* diminue cette productivité, mais il est évident que cette diminution désavantage nettement ces brouteurs. Comme *Elimia* était le principal invertébré, les résultats portent à croire que de faibles concentrations de bioéléments limitent la production primaire et secondaire en automne.

Received March 25, 1991
Accepted October 4, 1991
(JA963)

Reçu le 25 mars 1991
Accepté le 4 octobre 1991

Biomass accrual by periphyton is the integration of gains and losses. Biomass is gained primarily from in-place biosynthesis, although immigration can be important in early stages of lotic periphyton development (Bothwell and Jasper 1983; Stevenson 1986). Factors that influence biosynthesis in lotic periphyton have been moderately well studied, with much of the emphasis on nutrient limitation (e.g. Stockner and Shortreed 1978; Peterson et al. 1983; Bothwell 1985; Grimm and Fisher 1986; Pringle 1987). Losses of periphyton biomass occur due to consumption by grazers, dislodgement and export of cells by current, and mortality due to pathogens or senescence. Factors influencing biomass loss have generally received less attention than those that affect biomass gain, but grazing studies have recently become prominent (e.g. Lamberti and Resh 1983; Hill and Knight 1987; Stewart 1987; Feminella et al. 1989).

Nutrient limitation of lotic periphyton is a complex interaction of nutrient concentration, water velocity, competition, and diffusion. It was initially thought that nutrients did not limit algal growth in streams because flowing water provided a constant supply of new nutrients to attached algae (Wuhrmann 1974). Furthermore, Bothwell (1988) demonstrated that cellular growth rates of lotic periphyton saturated at nutrient concentrations much lower than found in most streams. To accommodate the abundant empirical evidence of nutrient limitation at concentrations above cellular saturation levels, it is necessary to invoke the effect of periphyton biomass on its own metabolism (Bothwell 1989). Even thin periphyton is a three–dimensional matrix of algae and microscopic heterotrophs surrounded by biogenic mucilage (Lock et al. 1984). Diffusion of nutrients through the overlying boundary layer and into this matrix is slow compared with stream flow, and the closely packed microorganisms within the matrix create a relatively high demand for metabolic substrates (e.g. Carlton and Wetzel 1987). Bothwell (1989) identified two types of growth versus nutrient curves for periphyton: (1) a rapidly saturating, Monod type evident in phytoplankton and early periphyton stages and (2) a more linear, slowly saturating type found in older periphyton. The latter diffusion-limited curve reflects the effect of biomass on periphyton productivity.

---

[1] Publication No. 3834, Environmental Sciences Division, Oak Ridge National Laboratory.

[2] Author to whom correspondence should be addressed.

The consumption of algal cells by grazers obviously diminishes productive periphyton biomass. However, positive effects of grazing on the periphyton left uneaten have been observed or implicated in a number of studies (Gregory 1983; Lamberti and Resh 1983; Hill and Knight 1987; Stewart 1987; Power et al. 1988; McCormick and Stevenson 1989, 1991; Hill and Harvey 1990). Grazers are thought to increase biomass-specific production of periphyton by recycling limiting nutrients, cropping senescent cells, selecting for the establishment of rapidly dividing algal taxa, or mitigating the self-shading and diffusion limitation associated with vertical biomass accrual. Some investigators have reported that positive indirect effects of grazing can outweight negative direct effects, so that net production in grazed communities exceeds that in ungrazed communities (Cooper 1973; Flint and Goldman 1975; Kesler 1981).

In this experiment, we examined the effects of nutrient limitation, grazing, and the potential interaction of nutrients and grazing on periphyton productivity in a headwater stream in eastern Tennessee. Many streams in this area have dense populations of grazing snails and low nutrient concentrations (e.g. Elwood et al. 1981), suggesting that primary production may be closely constrained by high loss rates and low photosynthetic rates. We experimentally excluded grazers and amended nutrient levels to determine if these factors alone or together limited periphyton biomass and production.

Materials and Methods

Study Site

White Oak Creek is a tributary of the Clinch River that flows through the Oak Ridge National Laboratory (35°55′N, 84°19′W), Tennessee, USA. This experiment was conducted in upper White Oak Creek (‘‘WOC 6.8″ in Loar et al. 1991), a relatively undisturbed second-order stream with an adjacent deciduous forest. Shading by streamside trees is extensive during summer, but light reaching the stream increases substantially after autumn leaf-fall. Like many headwater streams in eastern Tennessee, upper White Oak Creek has moderately alkaline water (approximately 120 mg $CaCO_3 \cdot L^{-1}$) and relatively low nutrient concentrations (Loar et al. 1991). Densities of the prosobranch snail *Elimia clavaeformis*, the predominant grazer, are quite high. Snail biomass is 10 times periphyton biomass (W. Hill, unpubl. data). Average water temperature in upper White Oak Creek during October is approximately 12°C (Loar et al. 1991).

Experimental Design

Nutrient additions and snail exclusions were performed in four Plexiglas channels (each 122 cm long, 30 cm wide, and 41 cm high) that were open at each end and on top. The channels were placed side by side on the stream bed in White Oak Creek with their longitudinal axes parallel to the current. Plastic mesh (6.4-mm openings) was attached to the upstream end of each channel to prevent drifting leaves from fouling experimental substrata. Surface velocity, measured by timing the transit of a leaf of watercress down each channel, averaged 7.6 $cm \cdot s^{-1}$.

Experimental substrata consisted of unglazed ceramic tiles (4.8 cm per side) that were conditioned in White Oak Creek for >1 yr before the experiment. The tiles were attached to bricks (seven tiles per brick) with silicon glue before conditioning. At the beginning of the experiment, tiles from half of the bricks were removed and secured with rubber bands to Plexiglas plates (seven tiles per plate) that were suspended approximately 5 cm above the channel bottoms with wires clamped to the channel sides. The seven tiles on each suspended Plexiglas plate were essentially inaccessible to grazing snails; each channel contained two suspended plates. Each channel also contained two bricks (with attached tiles) that were set on the bottom of the channel and were accessible to snails. The four sets of tiles in each channel were placed in a line parallel to the current, approximately 10 cm apart. Tiles suspended on the Plexiglas plates were kept at the same distance above the channel bottom as the tiles attached to bricks. Cobbles from the stream bed were added to the channels around the tiles to provide additional natural substratum for snails that entered the channels from the open downstream ends.

Nutrients were added to the upstream ends of two of the channels by dripping a stock solution of 50 g $KNO_3 \cdot L^{-1}$ and 7.6 g $K_2HPO_4 \cdot L^{-1}$ from a carboy placed nearby on the stream bank. Several bricks placed crosswise in the channels just downstream from the nutrient drip lines provided turbulence to mix the stock solution with water flowing into the two channels. Nutrient stock was added at a rate to increase nitrate and phosphate concentrations in the two channels 3–4 times background levels. Because nutrients were applied to whole channels that contained two types of tiles (grazed and ungrazed), the resulting design was a 2 × 2 split-plot factorial. Experimental units for nutrient effects were the channels whereas sets of tiles (four per channel, 16 total) served as experimental units for determining grazing effects and nutrient × grazing interactions.

Tiles were placed into the channels and nutrient amendments were begun on 6 October 1989. Beginning a week later, the snails on each set of tiles in each channel were counted daily until the end of the experiment. The few snails found on the suspended tiles were removed after counts were made. The positions of the four sets of tiles in each channel were changed every 2 d to minimize the potential effect of position within the channel. Nutrient concentrations in the channels were checked once during the experiment, and nutrient concentrations in White Oak Creek (immediately upstream from the channel location) were analyzed just before the experiment began and near its end 3 wk later. Nutrient concentrations were analyzed on a Lachat autoanalyzer using standard methods (Loar et al. 1991). Photosynthetically active radiation (PAR) was measured at midday on the day before the experiment ended with a LiCor quantum sensor held over the channels.

Periphyton Analyses

Tiles were collected from the channels on the morning of 27 October 1989, removed from the Plexiglas plates and bricks, and taken to the laboratory in water-filled containers. Periphyton was firmly attached to the tiles, and there was no visual evidence that it detached during the transfer to the laboratory or during subsequent photosynthetic measurements. Photosyn-

TABLE 1. Nutrient concentrations ($\mu g \cdot L^{-1}$) in upper White Oak Creek, autumn 1989. TN = total nitrogen, TP = total phosphorus, NO_3-N = nitrogen in the form of nitrate, SRP = soluble reactive phosphorus, N:P = molar ratio of NO_3-N/SRP.

Date	Sampling location	TN	TP	NO_3-N	SRP	N:P
26 Sept.	Stream	80	13	46	11	9.3
17 Oct.	Channel 1 (nutrients)	263	28	—	—	—
	Channel 2 (control)	60	8	—	—	—
	Channel 3 (control)	70	9	—	—	—
	Channel 4 (nutrients)	296	31	—	—	—
23 Oct.	Stream	119	14	32	5	14.2

thesis was measured at six irradiances: 44, 130, 250, 420, 590, and 1300 $\mu mol\ quanta \cdot m^{-2} \cdot s^{-1}$. To make these measurements, tiles were placed in circular glass chambers (19 cm diameter, 10 cm height) containing 900 mL of water from the appropriate channel. Individual pumps connected to the chambers provided recirculating flow at a velocity of approximately 30 $cm \cdot s^{-1}$ inside the chambers. The chambers were kept at 13°C in a water bath. A 100-W metal halide lamp with a phosphor-coated bulb provided light; the various irradiances were achieved by placing different numbers of neutral–density screens over individual chambers. One tile from each set of seven was exposed to one irradiance, so that each set received the entire range of irradiances.

Following a 15-min exposure to the experimental irradiance, 740 kBq of $NaH^{14}CO_3$ was injected into each chamber. Tiles were removed from the chambers 2 h after the ^{14}C was added, rinsed twice in stream water to remove unincorporated ^{14}C, and placed in jars containing 20 mL of dimethyl sulfoxide (DMSO). DMSO simultaneously extracts chlorophyll *a* and ^{14}C-labeled photosynthate (Palumbo et al. 1987). Extracted chlorophyll *a* was analyzed spectrophotometrically, and the concentration of chlorophyll *a* was calculated with the equations of Jeffrey and Humphrey (1975) and corrected for pheopigments. The validity of the Jeffrey and Humphrey (1975) extinction coefficients for chlorophyll *a* in DMSO was checked with pure chlorophyll *a* (Sigma). Extracted ^{14}C was counted in a Packard Tri-Carb 2000CA liquid scintillation analyzer, with quenching corrected by external standards. Nonphotosynthetic carbon uptake was determined in darkened chambers and subtracted from photosynthetic uptake.

Periphyton was brushed from the tiles with a toothbrush for the analysis of ash-free dry mass (AFDM) and algal biovolume. Except for four of the sets in which one tile was used as a dark control in the photosynthesis measurements, one tile from each set was brushed. Half of the brushed periphyton was dried on aluminum pans at 60°C, weighed, ashed at 480°C, and reweighed for AFDM determination. The other half was preserved in Lugol's solution and examined later with an inverted microscope. At least 500 individual cells or filaments in each sample were counted at 400× magnification. The average cell volume of each algal taxon was estimated by using average cell dimensions in appropriate geometric formulae.

Data Analysis

Photosynthesis–irradiance (P-I) data were fitted to the three-parameter photoinhibition model of Platt et al. (1980) with least-squares, nonlinear regression (SAS, PROC NLIN) (SAS 1985). In this model, $P = P_s(1 - e^{-a})e^{-b}$, where P is carbon uptake at a given irradiance (I), P_s is the theoretical maximum value of P in the absence of photoinhibition, $a = \alpha I/P_s$, $b = \beta I/P_s$, α is the slope of the initial linear portion of the curve,

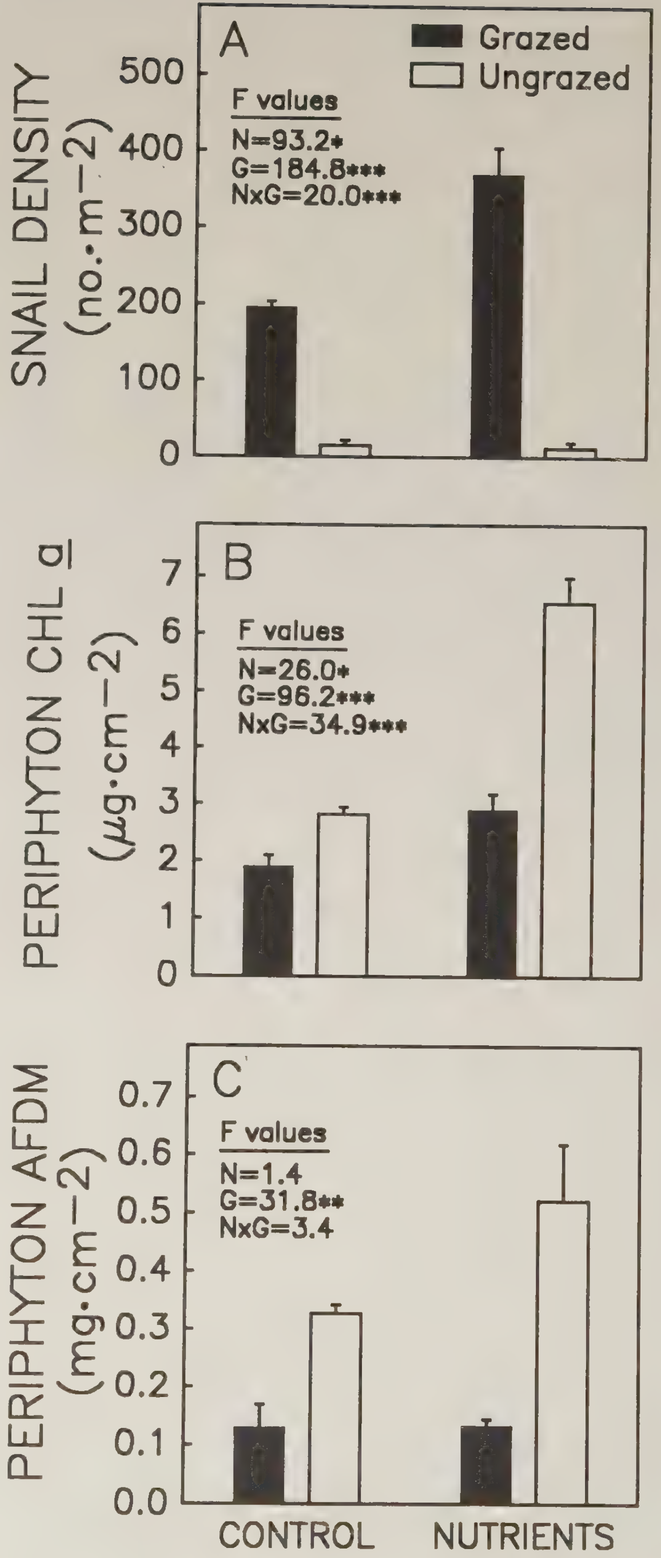


FIG. 1. Effects of experimental manipulations on (A) Snail density, (B) periphyton chloropyll *a*, and (C) periphyton AFDM. N = nutrients; G = grazing. Bars represent means ± 1 SE. *F* degrees of freedom from ANOVA of snail density and chlorophyll *a*: N = 1, 2; G = 1, 10; N X G = 1, 10. *F* degrees of freedom for AFDM: N = 1, 2; G = 1, 6; N × G = 1, 6. *$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

and β is a photoinhibition parameter. Four other P-I parameters, P_{max}, I_{max}, I_k, and T_b were calculated from the estimated model parameters as per Platt et al. (1980). P_{max} represents the maximum rate of carbon uptake, I_{max} is the irradiance at which P_{max} occurs, I_k estimates the onset of photosaturation, and I_b is the irradiance at which photoinhibition reduces P to 37% of P_s. Individual P-I models were generated for each set of tiles. P-I parameters from these models, as well as periphyton biomass and snail density parameters, were analyzed with a nested (split-plot) model (SAS, PROC GLM) (SAS 1985). Parameters were log transformed when variances were correlated with means.

Results

Approximately 95% of the leaves on streamside trees had fallen by the end of this experiment, allowing high irradiances on the stream bed. PAR measured over the channels on 26 October was 1400 μmol quanta$\cdot$m$^{-2}\cdot$s^{-1} at midday. Nitrate and soluble reactive phosphorus (SRP) concentrations in upper White Oak Creek were moderately low both before and near the end of the experiment (Table 1). Nutrient addition raised total nitrogen and phosphate concentrations 3–4 times that measured in control channels.

Average snail density on the experimental tiles was significantly affected by both treatment factors (Fig. 1A). Snails were abundant on tiles that were contiguous with the stream bed (''grazed'' tiles) whereas very few snails were found on the suspended tiles (''ungrazed'' tiles), confirming the efficacy of the grazer exclusion method. No grazers other than snails were observed on the tiles during the experiment. Grazed tiles in nutrient-enriched channels had 89% more snails than grazed tiles in control channels (Fig. 1A).

Snail grazing decreased periphyton chlorophyll *a*, particularly in the nutrient-enriched channels (Fig. 1B). Grazed periphyton in nutrient-enriched channels showed a modest, but statistically significant, increase over grazed periphyton in control channels. Tiles that were both ungrazed and enriched with nutrients accrued 2–3 times more chlorophyll *a* than the other treatment combinations, indicating a strong interaction between nutrients and grazing on periphyton biomass.

Grazing decreased periphyton AFDM regardless of nutrient regime (Fig. 1C). Overall nutrient effects were not significant ($P = 0.36$), and although ungrazed tiles in nutrient-enriched channels had the largest mean AFDM, the nutrient × grazing interaction was not significant ($P = 0.11$). Less statistical power was available for testing grazing and nutrient × grazing effects on AFDM than on chlorophyll *a* (6 error degrees of freedom versus 10) because four tiles were sacrificed for use in ^{14}C dark uptake controls.

Algal assemblages on the tiles were relatively simple. Five taxa comprised 84% of total algal biovolume (Table 2). *Stigeoclonium* sp. was the largest single contributor in all treatments. Several replicates of periphyton samples from the grazed tiles dried during storage, so statistical power was even more limited (only 4 error degrees of freedom for grazing and nutrient × grazing effects) than in the AFDM analysis. This limited power, and the great variability between replicates, explains why neither the grazing term nor the grazing × nutrient term in the ANOVA was significant, even though the mean *Stigeoclonium* biovolume on ungrazed tiles from enriched channels was 4–9 times greater than that on the grazed tiles. The biovolume of two diatoms, *Gomphonema dichotomum* and *Achnanthes minutissima*, was statistically greater on ungrazed tiles, however. Total algal biovolume was also significantly greater on ungrazed tiles than on grazed tiles. Neither nutrient nor nutrient × grazing effects on algal biovolume were statistically significant.

Substantial grazing and nutrient effects on areal-specific production were evident at all irradiances (Fig. 2A, 2B). Maximal photosynthetic rates increased >2 times when snails were excluded and increased >2 times when nutrients were added; P_{max} for ungrazed periphyton in enriched channels was approximately 5 times greater than grazed periphyton in control channels (Table 3). The slope (α) of the linear phase of the P-I relationship was affected by grazing and nutrient treatments in the same manner as P_{max}, so that α was >4 times larger for ungrazed, enriched periphyton than it was for grazed periphyton in control channels. The inhibition constant β was significantly larger for ungrazed periphyton, but was unaltered by nutrients. Grazing did not significantly affect either the irradiance at which saturation began (I_k) or the irradiance at which P_{max} occurred (I_{max}). The effect of nutrients in increasing I_{max} was nearly significant ($P = 0.07$), however. Nutrient addition caused approximately 2 times increase in I_b, the inhibition parameter independent of P_{max} (Platt et al. 1980), suggesting that periphyton from enriched channels experienced less photoinhibition than periphyton from control channels.

Grazing significantly depressed chlorophyll-specific productivity (Fig. 2C, 2D). Chlorophyll-specific P_{max} was 37 and 20% lower in control channels and nutrient-enriched channels, respectively (Table 3). Nutrient effects on chlorophyll-specific P_{max} were not significant, and although the mean P_{max} for grazed periphyton in nutrient-enriched channels was greater than the mean P_{max} for grazed periphyton in control channels, the grazing × nutrient interaction was not significant.

TABLE 2. Biovolumes ($10^6 \times \mu$m$^3\cdot$cm^{-2}) of major alga taxa on experimental substrates. Biovolume values are means ± 1 SE. Biovolumes (μm^3) per cell were: *Stigeoclonium* = 221, *Phomidium tenue* = 3, unidentified cyanophyte = 8, *Gomphonema dichotomum* = 1060, *Achnanthes minutissima* = 64. N = nutrients, G = grazing. $^*P < 0.05$, $^{**}P < 0.01$.

	Control		Nutrients		ANOVA *F* values		
	Grazed ($n = 1$)	Ungrazed ($n = 3$)	Grazed ($n = 3$)	Ungrazed ($n = 3$)	N^a	G^b	N × G^b
Stigeoclonium sp.	11.6	24.9 ± 8.8	6.9 ± 2.4	104.9 ± 75.6	0.23	3.00	1.44
Phormidium tenue	1.2	7.0 ± 3.0	1.5 ± 0.7	7.3 ± 3.9	0.39	3.80	0.69
Unidentified cyanophyte	0.9	0.5 ± 0.1	0.9 ± 0.3	0.9 ± 0.6	0.10	1.44	0.42
Gomphonema dichotomum	0.4	17.3 ± 6.2	0.3 ± 0.3	21.1 ± 14.1	2.08	8.02*	1.12
Achnanthes minutissima	0.2	1.6 ± 0.5	0.2 ± 0.1	3.2 ± 1.5	0.65	27.73**	1.82
Total biovolume	20.0	60.5 ± 21.8	10.7 ± 4.1	155.9 ± 97.1	0.37	10.14*	2.75

$^aF_{1,2}$.
$^bF_{1,4}$.

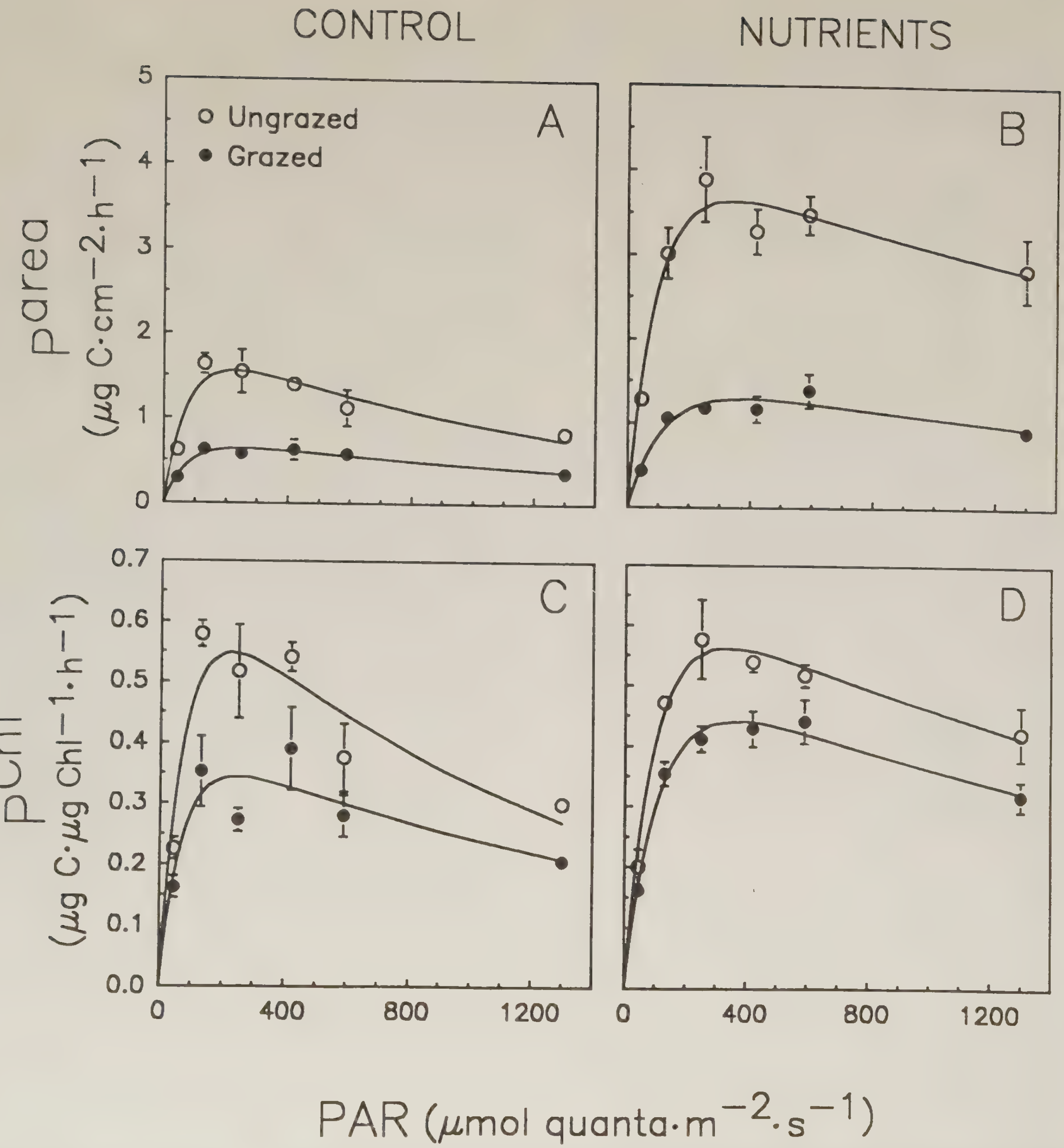


FIG. 2. Periphyton carbon uptake. P^{area} = areal-specific uptake; P^{Chl} = chlorophyll *a* specific uptake; PAR = photosynthetically active radiation. Values are means ± 1 SE (n = 4). Photosynthesis–irradiance curves were fit using the three-parameter photoinhibition model to Platt et al. (1980).

Discussion

Biomass Response

The results of this experiment demonstrate that snail grazing can limit periphyton accrual in White Oak Creek. All three biomass parameters (chlorophyll *a*, AFDM, and biovolume) increased when snails were excluded from experimental substrata, especially in nutrient-enriched channels. Grazing has been shown to limit periphyton accrual in many other in situ experiments (e.g. Lamberti and Resh 1983; McAuliffe 1984; Hill and Knight 1987, 1988a; Feminella et al. 1989; Feminella and Resh 1990), and in this experiment, snails limited periphyton biomass to low levels even in nutrient-enriched channels. The added production provided by nutrient enrichment appeared to be channeled into increased grazer production. Our results are similar to those of Stewart (1987), who found that the grazing minnow *Campostoma* kept pace with nutrient-stimulated algal growth and maintained steady periphyton biomass despite increased productivity.

TABLE 3. Photosynthesis–irradiance parameters calculated for tiles from individual bricks; $n = 4$ for each treatment combination. Values are means ± 1 SE. N = nutrients, G = grazing. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

	Control		Nutrients		ANOVA F values		
	Grazed	Ungrazed	Grazed	Ungrazed	N[a]	G[b]	N × G[b]
$P_{\max}$ (area)[c]	0.68 ± 0.09	1.67 ± 0.23	1.31 ± 0.13	3.75 ± 0.35	40.13*	67.02**	0.43
α (area)[d]	10 ± 2	25 ± 1	14 ± 8	44 ± 3	37.62*	117.05***	0.56
β (area)[d]	0.5 ± 0.1	1.6 ± 0.5	0.6 ± 0.1	1.2 ± 0.1	0.58	14.50**	0.37
$P_{\max}$ (Chl)[e]	0.37 ± 0.05	0.59 ± 0.06	0.47 ± 0.03	0.59 ± 0.02	1.51	15.52**	1.36
α (Chl)[f]	5.5 ± 0.8	9.0 ± 0.5	4.7 ± 0.4	6.8 ± 0.7	1.59	42.95***	2.65
β (Chl)[f]	0.2 ± 0.1	0.5 ± 0.2	0.2 ± 0.02	0.2 ± 0.1	5.41	2.95	1.86
$I_{\max}$[g]	255 ± 25	222 ± 14	349 ± 36	339 ± 15	13.04	0.77	0.49
I_k[g]	72 ± 11	66 ± 9	95 ± 15	86 ± 5	4.96	0.36	0.00
I_b[g]	1650 ± 30	1240 ± 170	2600 ± 530	3060 ± 360	416.10***	0.05	1.84

[a] 1, 2 degrees of freedom.
[b] 1,10 degrees of freedom.
[c] $\mu g\ C \cdot cm^{-2} \cdot h^{-1}$.
[d] $(ng\ C \cdot cm^{-2} \cdot h^{-1}) \cdot (\mu mol\ quanta \cdot m^{-2} \cdot s^{-1})^{-1}$.
[e] $\mu g\ C \cdot \mu g\ Chl\ a^{-1} \cdot h^{-1}$.
[f] $(ng\ C \cdot \mu g\ Chl\ a^{-1} \cdot h^{-1}) \cdot (\mu mol\ quanta \cdot m^{-2} \cdot s^{-1})^{-1}$.
[g] $\mu mol\ quanta \cdot m^{-2} \cdot s^{-1}$.

Snails maintained low levels of periphyton biomass in nutrient-enriched channels at least partly because of a numerical response. Snails were 89% more abundant on tiles in nutrient-enriched channels, presumably exerting a grazing pressure proportional to their density. The similarity between the increase in snail density (89%) and the increase in productivity (92% higher areal-specific $P_{\max}$) in nutrient-enriched channels suggests that snail density closely tracked local variations in primary productivity. Snail response to increased periphyton productivity was apparently mediated by a subtle cue, as periphyton biomass and taxonomic composition were very similar on grazed tiles in control and nutrient-enriched channels. Differences in snail reproduction within control and nutrient-enriched channels could not have caused the different snail densities because all snails counted on the tiles were orders of magnitude larger than 3-wk-old snails.

Taxonomic Response

Periphyton communities experiencing heavy grazing pressure by invertebrates are characteristically dominated by adnate algae that have a refuge close to the substratum (Sumner and McIntire 1982; Hill and Knight 1987; Steinman et al. 1987; Lowe and Hunter 1988; DeNicola et al. 1990). In streams like White Oak Creek where grazing snails are very abundant, basal cells of *Stigeoclonium* often dominate the periphyton (Stock and Ward 1989). These prostrate cells appear to be grazer resistant (Steinman et al. 1987; Steinman 1991) and may depend on grazers to remove overgrowing taxa that could diminish their access to light and nutrients (McCormick and Stevenson 1989). In this experiment, however, *Stigeoclonium* did not suffer in the absence of grazing. Potential competitors (especially the diatoms *Gomphonema dichotomum* and *Achnanthes minutissima*) were considerably more abundant in ungrazed periphyton, yet mean biovolume densities of *Stigeoclonium* were also several times larger on ungrazed tiles. The high variability of this alga in nutrient-enriched channels and the limited statistical power in the ANOVA (1,4 degrees of freedom) resulted in grazing effects that were not statistically significant ($F = 3.00$, $P < 0.16$), but *Stigeoclonium* was the major contributor to the statistically significant increase in total algal biovolume when snails were excluded (Table 2). We therefore cannot confirm the deleterious effect of grazer removal on *Stigeoclonium* abundance reported by McCormick and Stevenson (1989, 1991). In habitats like White Oak Creek, where algal biomass is very low, it may require more than 3 wk for other algae to accumulate and replace *Stigeoclonium* when snails are excluded.

Productivity Responses

In contrast with biomass, primary productivity was significantly affected by both grazing and nutrients. These two factors appeared to operate simultaneously, for areal-specific productivity was significantly increased by relaxing the constraint of either factor. The simultaneous, rather than hierarchical, effect of grazing and nutrients may be the result of these factors acting on different parts of the periphyton carbon budget. Grazers increase loss rates by consuming and dislodging productive algal cells, while nutrients operate to increase rates of biosynthesis. Although the removal of algal biomass was probably the largest effect of snails, they also reduced areal-specific productivity by lowering biomass-specific productivity.

The prevailing view in stream ecology is that positive indirect effects mitigate at least some of the negative effects of biomass loss caused by grazing. This view is supported by numerous reports of grazing-induced increases in chlorophyll-specific or AFDM-specific productivity (Gregory 1983; Lamberti and Resh 1983; Lamberti et al. 1987; Stewart 1987; Hill and Harvey 1990) and even a few reports of grazing-increased areal-specific productivity (Cooper 1973; Kesler 1981; Flint and Goldman 1975). The decreased chlorophyll-specific productivity caused by *Elimia* in this experiment was therefore unexpected, especially since snails markedly reduced periphyton biomass. Due to self-limitation within periphyton communities, biomass-specific primary production is highest when biomass is low (Pfeifer and McDiffett 1975; Marker 1976; Hudon et al. 1987). At low biomass, individual cells within the periphyton matrix are less likely to suffer from shading and nutrient depletion by overlying cells and consequently exhibit high biomass-specific productivity (Hill and Boston 1991).

The mechanism behind *Elimia*'s depression of biomass-specific productivity is unclear. One possible explanation is that *Stigeoclonium* basal cells are particularly inefficient photosynthetically. They may funnel energy and resources into protective mechanisms or features that allow persistence under intense grazing pressure and are consequently unable to invest those resources in photosynthetic enzymes and pigments. Prostrate forms of marine algae that persist under intense grazing have lower growth rates than upright forms (Lubchenco and Cubit 1980). However, grazing by *Elimia* also depresses biomass-specific productivity in periphyton dominated by diatoms (Mulholland et al. 1983) and cyanophytes (W. R. Hill, unpubl. data), indicating that *Stigeoclonium* does not have a unique response to grazing by *Elimia*. A second possibility is that mucus deposited by grazing *Elimia* may contain substances that inhibit periphyton metabolism, but gastropod mucus is usually regarded as a source of nitrogen and other stimulatory nutrients (e.g. Calow 1979; Connor and Quinn 1984; Herndl and Peduzzi 1989). A third possibility is that intense grazing by snails removes most algal cells except those that are in cracks and crevices in the substratum. These recessed cells may have reduced access to light or metabolic substrates (carbon, nutrients) and consequently exhibit low photosynthetic rates.

The direct experimental evidence for nutrient limitation was very strong. Although we did not perform indirect analyses (e.g. assays of alkaline phosphatase activity or periphyton elemental composition) that could corroborate nutrient limitation, nutrient enrichment significantly increased (1) snail density, (2) periphyton biomass where snails were excluded, and (3) areal-specific productivity of both grazed and ungrazed periphyton. These effects were statistically significant despite low statistical power available to detect nutrient effects (only 2 error degrees of freedom in the split-plot ANOVA). The absence of statistically significant nutrient effects on chlorophyll-specific productivity is inconsistent with the other strong indicators of nutrient limitation, but may be explained by low statistical power or increased chlorophyll *a* per cell in nutrient-enriched periphyton. Increases in cellular-specific chlorophyll *a* concentration commonly occur in nitrogen–efficient algae when nitrogen is added (Thomas and Dodson 1972; Osborne and Geider 1986; Cleveland and Perry 1987), and increases in cellular concentrations of chlorophyll *a* can obscure biomass-specific photosynthetic rates when chlorophyll *a* is used to normalize photosynthetic rates (Prezelin 1981). Increased chlorophyll *a* per cell could also explain why nutrient enrichment increased total chlorophyll *a* (micrograms per square centimetre of substrate) in grazed periphyton, but not AFDM or biovolume. There was no direct evidence, however, that the periphyton was nitrogen deficient.

We could not specify whether nitrogen or phosphorus limited productivity in White Oak Creek because our enrichments contained both nutrients. The N:P ratio in unamended White Oak Creek water at the end of the experiment was very close to the Redfield (1958) ratio of 15 that has been used to delimit the boundary between nitrogen and phosphorus limitation. Periphyton productivity in White Oak Creek may be alternately limited by either nutrient, depending on the temporal and spatial variability of the N:P ratio. Algal cells in any one location could be simultaneously limited by nitrogen and phosphorus, and the strong productivity response we observed in this experiment may have required both nutrients.

Despite the strength of the experimental evidence, it is somewhat surprising that periphyton as sparse as that in White Oak Creek could be nutrient limited. Flowing water provides constant renewal of nutrients (Wuhrmann 1974), so supply rates of nitrogen and phosphorus to attached cells should be adequate unless biomass develops to the point that a nutrient diffusion gradient exists within the periphyton (Bothwell 1989). Periphyton on both grazed and ungrazed substrates exhibited little vertical development (<1 mm), and concentrations of nitrogen and phosphorus in White Oak Creek were only moderately low. Inherently high requirements for nutrients by the dominant taxa, *Stigeoclonium*, may be the reason why nutrient addition increased productivity of our thin periphyton. Filamentous green algae generally have relatively high extracellular requirements for nitrogen and phosphorus (Francke and Den Oude 1983; Horner et al. 1983; Bothwell 1989), and Rosmarin (1983) reported that the growth rate of *Stigeoclonium tenue* saturated at approximately 30 μg P·L^{-1}, a concentration several times greater than SRP in White Oak Creek. Thus, nutrient limitation in this experiment may have occurred because of Monod type kinetics at the cellular level instead of diffusion kinetics at the community level (Bothwell 1989).

We would like to emphasize that this experiment was performed just after leaf fall, a time when nutrients are most likely to be limiting. Nutrient demand by heterotrophic microbes on leaves is maximum within 20–30 d after leaf fall and presumably reduces the supply of nutrients to periphyton (Mulholland et al. 1984, 1985). More importantly, PAR reaching the stream bed had risen from <50 to >1300 μmol quanta·m^{-2}·s^{-1} with the loss of canopy leaves. Nutrients are not likely to limit productivity when canopy leaves are present, as periphyton photosynthesis in shaded eastern Tennessee streams saturates above 100 μmol quanta·m^{-2}·s^{-1} (Boston and Hill 1991). Summertime experiments in White Oak Creek (W. R. Hill, unpubl. data), nearby Ish Creek (Hill and Harvey 1990), and Walker Branch (A. D. Steinman, unpubl. data) have demonstrated that periphyton productivity is very strongly light dependent. Several studies in shaded oligotrophic streams have shown that light must first be augmented before nutrient amendments have any effect on periphyton biomass or productivity (Gregory 1980; Triska et al. 1983; Hill and Knight 1988b). The relatively warm water temperature in early autumn probably accentuates nutrient demand by both autotrophic and heterotrophic microbes in White Oak Creek.

Photosynthesis–irradiance responses were not strongly affected by grazing or nutrients. We hypothesized that photosynthesis would saturate at higher light intensites as biomass accrual was released from grazing (Paul and Duthie 1989), but neither the onset of saturation (I_k) nor the irradiance of maximum photosynthesis ($I_{\max}$) was significantly influenced by grazing. This lack of grazing effect is not altogether surprising, as even the biomass of the ungrazed, enriched periphyton was low compared with that found in other habitats. There was some evidence of moderate self-shading induced by nutrient enrichment: periphyton in nutrient-enriched channels had higher $I_{\max}$ values that were nearly significant (with only 2 error degrees of freedom) and appeared less susceptible to photoinhibition (significantly greater I_b' values). Nutrient-induced self-shading may have been caused by increased cellular pigment levels (Osborne and Geider 1986; Cleveland and Perry 1987; Herzig and Falkowski 1989). The slope of the light-limited portion of the P-I curve (α) and the photoinhibition constant (β) were strongly affected by grazing and nutrients, but the interpretation of these effects is confounded by the dependence of these parameters on $P_{\max}$ (Platt et al. 1980; Hill and Boston 1991).

Despite considerable research on nutrient spiralling at the Oak Ridge National Laboratory, sustained increases in periphyton biomass as a result of in situ nutrient amendments have not been reported for eastern Tennessee streams. Elwood et al. (1981) suggested that the immigration of additional grazers

(*Elimia*) was responsible for the failure of their unreplicated phosphorus addition to maintain higher levels of periphyton biomass in Walker Branch. Our results in nearby White Oak Creek support both the potential of nutrient limitation and the ability of *Elimia* to respond numerically to localized increases in productivity. Increases in primary productivity on larger scales (e.g. the entire stream), however, would require significant functional responses by grazers to control periphyton biomass over the short term. *Elimia* is food limited and appears to have submaximal ingestion rates in White Oak Creek (W. Hill, unpubl. data), so a functional response of some magnitude to increased productivity is probable. Over the long term, *Elimia* would probably respond to increased primary production with increased reproduction. Long term diminishment of physicochemical constraints on primary production should be manifest in increased grazer biomass rather than increased periphyton biomass when grazers are food limited.

Acknowledgements

Art Stewart, Pat Mulholland, Gordon Robinson, and an anonymous reviewer provided constructive comments on the manuscript. This research was sponsored by the Environmental Restoration and Waste Management Program, U.S. Department of Energy, under contract No. DE-AC05-840R21400 with Martin Marietta Energy Systems, Inc. W. R. Hill and A. D. Steinman were supported by appointments to the U.S. Department of Energy Laboratory Cooperative Postgraduate Training Program administered by Oak Ridge Associated Universities.

References

Boston, H. L., and W. R. Hill. 1991. Photosynthesis–light relations of stream periphyton communities. Limnol. Oceanogr. 36: 644–656.

Bothwell, M. L. 1985. Phosphorus limitation of lotic periphyton growth rates: an intersite comparison using continuous-flow troughs (Thompson River system, British Columbia). Limnol. Oceanogr. 30: 527–542.

1988. Growth rate responses of lotic periphytic diatoms to experimental phosphorus enrichment: the influence of temperature and light. Can. J. Fish. Aquat. Sci. 261–270.

1989. Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. Can. J. Fish. Aquat. Sci. 46: 1293–1301.

Bothwell, M. L., and S. Jasper. 1983. A light and dark trough methodology for measuring rates of lotic periphyton settlement and net growth: an evaluation through intersite comparison, p. 253–265. *In* R. G. Wetzel [ed.] Periphyton of freshwater ecosystems. Dr. W. Junk Publishers, The Hague, The Netherlands.

Calow, P. 1979. Why some metazoan mucus secretions are more susceptible to microbial attack than others. Am. Nat. 114: 149–152.

Carlton, R. G., and R. G. Wetzel. 1987. Distributions and fates of oxygen in periphyton communities. Can. J. Bot. 65: 1031–1037.

Cleveland, J. S., and M. J. Perry. 1987. Quantum yield, relative specific absorption and fluorescence in nitrogen-limited *Chaetoceros gracilis*. Mar. Biol. 94: 489–497.

Connor, V. M., and J. F. Quinn. 1984. Stimulation of food species growth by limpet mucus. Science (Wash., DC) 225: 843–844.

Cooper, D. C. 1973. Enhancement of net primary productivity by herbivore grazing in aquatic laboratory microcosms. Limnol. Oceanogr. 18: 31–37.

DeNicola, D. M., C. D. McIntire, G. A. Lamberti, S. V. Gregory, and L. R. Ashkenas. 1990. Temporal patterns of grazer–periphyton interactions in laboratory streams. Freshwater Biol. 23: 475–489.

Elwood, J. W., J. D. Newbold, A. F. Trimble, and R. W. Stark. 1981. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary production. Ecology 62: 146–158.

Feminella, J. W., M. E. Power, and V. H. Resh. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. Freshwater Biol. 22: 445–457.

Feminella, J. W., and V. H. Resh. 1990. Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. Ecology 71: 2083–2094.

Flint, R. W., and C. R. Goldman. 1975. The effects of a benthic grazer on the primary productivity of the littoral zone of Lake Tahoe. Limnol. Oceanogr. 20: 935–944.

Francke, J. A., and P. J. Den Oude. 1983. Growth of *Stigeoclonium* and *Oedogonium* species in artificial ammonium-N and phosphate-P gradients. Aquat. Bot. 15: 375–380.

Gregory, S. V. 1980. Effects of light, nutrients, and grazing on periphyton communities in streams. Ph.D. thesis, Oregon State University, Corvallis, OR. 154 p.

1983. Plant–herbivore interactions within stream populations and communities, p. 157–189. *In* J. R. Barnes and G. W. Minshall [ed.] Stream ecology. Application and testing of general ecological theory. Plenum, New York, NY.

Grimm, N. B., and S. G. Fisher. 1986. Nitrogen limitation in a Sonoran Desert stream. J. N. Am. Benthol. Soc. 5: 2–15.

Herndl, G. J., and P. Peduzzi. 1989. Potential microbial utilization rates of sublittoral gastropod mucus trails. Limnol. Oceanogr. 34: 780–784.

Herzig, R., and P. G. Falkowski. 1989. Nitrogen limitation in *Isochrysis galgana* (Haptophyceae). I. Photosynthetic energy conversion and growth efficiencies. J. Phycol. 25: 462–471.

Hill, W. R., and H. L. Boston. 1991. Community development alters photosynthesis–irradiance relations in stream algae. Limnol. Oceanogr. 36: 1375–1389.

Hill, W. R., and B. C. Harvey. 1990. Periphyton responses to higher trophic levels and light in a shaded stream. Can. J. Fish. Aquat. Sci. 47: 2307–2314.

Hill, W. R., and A. W. Knight. 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68: 1955–1965.

1988a. Concurrent grazing effects of two stream insects on periphyton. Limnol. Oceanogr. 33: 15–26.

1988b. Nutrient and light limitation of algae in two northern California streams. J. Phycol. 24: 125–132.

Horner, R. R., E. B. Welch, and R. B. Veenstra. 1983. Development of nuisance periphytic algae in laboratory streams in relation to enrichment and velocity, p. 121–134. *In* R. G. Wetzel [ed.] Periphyton of freshwater ecosystems. Dr. W. Junk Publishers, The Hague, The Netherlands.

Hudon, C., H. C. Duthie, and B. Paul. 1987. Physiological modifications related to density increase in periphytic assemblages. J. Phycol. 23: 393–399.

Jeffrey, S. W., and G. F. Humphrey. 1975. New spectrophotometric equations for determining chlorophylls a, b_1, c_1, c_2 in higher plants, algae, and natural phytoplankton. Biochem. Physiol. Pflanz. 167: 191–194.

Kesler, D. H. 1981. Periphyton grazing by *Amnicola limosa*: an enclosure–exclosure experiment. J. Freshwater Ecol. 1: 51–59.

Lamberti, G. A., L. R. Ashkenas, S. V. Gregory, and A. D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. J. N. Am. Benthol. Soc. 6: 92–104.

Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64: 1124–1135.

Loar, J. M., H. L. Boston, and R. D. Bailey. 1991. Water quality. *In* J. M. Loar [ed.] Fourth annual report on the ORNL biological monitoring and abatement program. ORNL/TM. Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN.

Lock, M. A., R. R. Wallace, J. W. Costerton, R. M. Ventullo, and S. E. Charlton. 1984. River epilithon: toward a structural–functional model. Oikos 42: 10–22.

Lowe, R. L., and R. D. Hunter. 1988. Effect of grazing by *Physa integra* on periphyton community structure. J. N. Am. Benthol. Soc. 7: 29–36.

Lubchenco, J., and J. Cubit. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. Ecology 61: 676–687.

Marker, A. F. H. 1976. The benthic algae of some streams in southern England: II. The primary production of the epilithon in a small chalk-stream. J. Ecol. 64: 359–373.

McAuliffe, J. R. 1984. Resource depression by a stream herbivore; effects on distributions and abundances of other grazers. Oikos 42: 327–333.

McCormick, P. V., and R. J. Stevenson. 1989. Effects of snail grazing on benthic algal community structure in different nutrient environments. J. N. Am. Benthol. Soc. 8: 162–172.

1991. Grazer control of nutrient availability in the periphyton. Oecologia.

Mulholland, P. J., J. W. Elwood, J. D. Newbold, J. R. Webster, L. A. Ferren, and R. E. Perkins. 1984. Phosphorus uptake by decomposing leaf detritus: effect of microbial biomass and activity. Verh. Int. Ver. Limnol. 22: 1899–1905.

Mulholland, P. J., J. D. Newbold, J. W. Elwood, L. A. Ferren, and J. R. Webster. 1985. Phosphorus spiralling in a woodland stream: seasonal variations. Ecology 66: 1012–1023.

Mulholland, P. J., J. D. Newbold, J. W. Elwood, and C. L. Hom. 1983. The effect of grazing intensity on phosphorus spiralling in autotrophic streams. Oecologia 58: 358–366.

Osborne, B. A., and R. J. Geider. 1986. Effect of nitrate-nitrogen limitation on photosynthesis of the diatom *Phaeodactylum tricornutum* Bohlin (Bacillariophyceae). Plant Cell Environ. 9: 617–625.

Palumbo, A. V., P. J. Mulholland, and J. W. Elwood. 1987. Extraction with DMSO to simultaneously measure periphyton photosynthesis, chlorophyll, and ATP. Limnol. Oceanogr. 32: 464–471.

Paul, B. J., and H. C. Duthie. 1989. Nutrient cycling in the epilithon of running waters. Can. J. Bot. 67: 2302–2309.

Peterson, B. J., J. E. Hobbie, T. L. Corliss, and K. Kriet. 1983. A continuous-flow periphyton bioassay: tests of nutrient limitation in a tundra stream. Limnol. Oceanogr. 28: 583–591.

Pfeifer, R. F., and W. F. McDiffett. 1975. Some factors affecting primary productivity of stream riffle communities. Arch. Hydrobiol. 75: 306–317.

Platt, T., C. L. Gallegos, and W. G. Harrison. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. J. Mar. Res. 38: 687–701.

Power, M. E., A. J. Stewart, and W. J. Matthews. 1988. Grazer control of algae in an Ozark Mountain stream: effects of short term exclusions. Ecology: 69: 1894–1898.

Prezelin, B. B. 1981. Light reactions in photosynthesis, p. 1–43. *In* T. Platt [ed.] Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210.

Pringle, C. M. 1987. Effects of water and substratum nutrient supplies on lotic periphyton growth: an integrated bioassay. Can. J. Fish. Aquat. Sci. 44: 619–629.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. Am. Sci. 46: 205–221.

Rosmarin, A. S. 1983. Direct examination of growing filaments to determine phosphate growth kinetics in *Cladophora glomerata* (L.) Kutz and *Stigeoclonium tenue* (Agardh) Kutz, p. 111–119. *In* R. G. Wetzel [ed.] Periphyton of freshwater ecosystems. Dr. W. Junk Publishers, The Hague, The Netherlands.

SAS. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute, Cary, NC. 956 p.

Steinman, A. D. 1991. Effects of herbivore size and hunger level on periphyton communities. J. Phycol. 27: 54–59.

Steinman, A. D., C. D. McIntire, S. V. Gregory, G. A. Lamberti, and L. R. Ashkenas. 1987. Effects of herbivore type and density on taxonomic structure and physignomy of algal assemblages in laboratory streams. J. N. Am. Benthol. Soc. 6: 175–188.

Stevenson, R. J. 1986. Mathematical model of epilithic diatom accumulation, p. 323–336. *In* M. Ricard [ed.] Proceedings of the Eighth International Diatom Symposium. Koeltz Scientific Books, Koenigstein.

Stewart, A. J. 1987. Responses of stream algae to grazing minnows and nutrients: a field test for interactions. Oecologia 72: 1–7.

Stock, M. S., and A. K. Ward. 1989. Establishment of a bedrock epilithic community in a small stream: microbial (alga and bacterial) metabolism and physical structure. Can. J. Fish. Aquat. Sci. 46: 1874–1883.

Stockner, J. G., and K. R. S. Shortreed. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. J. Fish. Res. Board Can. 35: 28–34.

Summer, W. T., and C. D. McIntire. 1982. Grazer–periphyton interactions in laboratory streams. Arch. Hydrobiol. 93: 135–157.

Thomas, W. H., and A. N. Dodson. 1972. On nitrogen deficiency in tropical oceanic phytoplankton. II. Photosynthetic and cellular characteristics of a chemostat-grown diatom. Limnol. Oceanogr. 17: 515–523.

Triska, F. J., V. C. Kennedy, R. J. Avanzino, and B. N. Reilly. 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages, p. 129–59. *In* T. D. Fontaine III and S. M. Bartell [ed.] Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, MI.

Wuhrmann, K. 1974. Some problems and perspectives in applied limnology. Mitt. Ver. Theor. Angew. Limnol. Verh. 20: 324–402.

Neomysis americana (Crustacea: Mysidacea) as an Intermediate Host for Sealworm, *Pseudoterranova decipiens* (Nematoda: Ascaridoidea), and Spirurid Nematodes (Acuarioidea)

David J. Marcogliese

Department of Fisheries and Oceans, Maurice Lamontagne Institute, P.O. Box 1000, Mont-Joli, Que. G5H 3Z4, Canada

Marcogliese, D. J. 1992. *Neomysis americana* (Crustacea: Mysidacea) as an intermediate host for sealworm, *Pseudoterranova decipiens* (Nematoda: Ascaridoidea), and spirurid nematodes (Acuarioidea). Can. J. Fish. Aquat. Sci. 49: 513–515.

Amphipods (*Gammarus oceanicus*) and mysids (*Neomysis americana*) were collected from three brackish ponds on Sable Island, 290 km east of Halifax, Nova Scotia. Thirteen nematodes were recovered from 3950 mysids subjected to enzymatic digestion. Four of the nematodes were identified as larval sealworm (*Pseudoterranova decipiens*). The remaining nematodes belong to two species: *Paracuaria adunca* and *Cosmocephalus obvelatus* (Acuarioidea). This is the first record of *N. americana* as an intermediate host for *P. decipiens*. It is also the first report of a mysid as intermediate host for either of the acuarioid nematodes and the first evidence of these two nematodes undergoing part of their life cycles in brackish or marine conditions. No nematodes were observed in 2364 amphipods or 1462 mysids examined microscopically, but unidentified metacercariae were found in 1.9% of the amphipods.

Des amphipodes (*Gammarus oceanicus*) et des mysidacés (*Neomysis americana*) ont été recueillis dans trois étangs saumâtres de l'île de Sable, située à 290 km à l'est d'Halifax (Nouvelle-Écosse). Des 13 nématodes obtenus de la digestion enzymatique de 3 950 mysidacés, quatre ont été identifiés comme des larves de ver du phoque (*Pseudoterranova decipiens*). Les autres nématodes appartenaient à deux espèces, soit : *Paracuaria adunca* et *Cosmocephalus obvelatus* (Acuarioidea). Ceci est la première fois que *N. americana* est identifiée comme hôte intermédiaire de *P. decipiens* et qu'un mysidacé est signalé comme hôte intermédiaire de ces deux nématodes de l'ordre des Acuarioidea. De plus, la présence de ces deux nématodes en eau salée ou saumâtre pendant une partie de leur cycle biologique est démontrée pour la première fois. Aucun nématode n'a été observé chez les 2 364 amphipodes et les 1 462 mysidacés qui ont fait l'objet d'un examen microscopique, mais des métacercaires non identifiées ont été observées chez 1,9 % des amphipodes.

Received May 13, 1991
Accepted October 4, 1991
(JB034)

Reçu le 13 mai 1991
Accepté le 4 octobre 1991

The sealworm *Pseudoterranova decipiens* (Nematoda: Anisakinae) is a stomach parasite of phocids, the larvae of which infect over 60 species of groundfish in North Atlantic waters, including 43 species in Canadian waters alone (McClelland et al. 1990). The cost to the fishing industry of removing sealworm from commercial fish fillets was estimated to be $30 million in Atlantic Canada alone in 1984 (Malouf 1986).

Despite the economic importance of this parasite in North Atlantic waters, and a variety of recent studies (McClelland et al. 1983a, 1983b, 1985, 1987; Bowen 1990), little is known of its life cycle under natural conditions. It has been suggested that a meiofaunal crustacean host, such as an harpacticoid copepod, is necessary for early development of the parasite, while a macroinvertebrate is required for transmission to fish, as the parasite in copepods does not attain sufficient size to be infective to vertebrate hosts (McClelland 1990). Serial transmission from copepods and small amphipods to larger crustaceans has been demonstrated experimentally (McClelland 1990). Presumably, fish acquire the parasite by ingesting infected macroinvertebrates (McClelland et al. 1983a) or by ingesting infected fish (Scott 1954; Burt et al. 1990). While a variety of macroinvertebrates, including amphipods, mysids, isopods, cumaceans, mud shrimp, polychaetes, and gastropods, have been infected in the laboratory (McClelland 1990), there are few reports of *P. decipiens* from naturally infected invertebrates.

Wallace Lake, a brackish pond located on Sable Island, 290 km east of Halifax, Nova Scotia, is frequented in summer by relatively high numbers (60–100) of harbour seals (*Phoca vitulina*), which are known to be infected with *P. decipiens* (Scott and Fisher 1958). Examination of fourspine stickleback (*Apeltes quadracus*) from Wallace Lake in the summer of 1989 revealed the presence of larval sealworm (D. J. Marcogliese, unpubl. data). Sealworm infection in fish from the pond indicates that the life cycle of *P. decipiens* can proceed from the egg at least as far as the fish host in Wallace Lake. Thus, macroinvertebrates were collected from Wallace Lake and other ponds on Sable Island to determine which species serve as intermediate hosts for *P. decipiens*. In this study, a new invertebrate host for sealworm and a new intermediate host for other nematode parasites are documented.

Materials and Methods

Amphipods (*Gammarus oceanicus*) were collected from Wallace Lake in baited minnow traps lined with 1-mm Nitex in August and December 1989 and in August 1990. Amphipods were also trapped from a pond adjacent to Wallace Lake and Middle Wallace Lake, located 3.5 km east of Wallace Lake, in August 1990. Mysids (*Neomysis americana*) were taken by dip net from Wallace Lake, the pond, and Middle Wallace Lake in August 1990.

Animals captured in August 1989 were fixed in 5% glycerol in 70% ethanol, subsequently cleared in lactic acid for 24 h, and examined under a stereomicroscope. Amphipods collected in December 1989 and August 1990 were examined live for parasites under a stereomicroscope. Mysids were either examined live microscopically or digested in 7 g of pepsin, 4 mL of concentrated HCl, and 6 g of NaCl in 1000 mL of water in a Baermann apparatus. The filtrate was examined periodically over a 24-h period.

Nematodes were measured under a Leitz Diaplan compound microscope with a calibrated ocular micrometer. All measurements are in millimetres. Measurements of the buccal cavity, nerve ring, and excretory pore refer to the distance from the anterior end.

Results

Thirteen nematodes were recovered from a total of 3950 mysids digested in a Baermann apparatus (Table 1). These nematodes occurred in mysids taken from Wallace Lake and Middle Wallace Lake. No parasites were observed microscopically in mysids.

Four of the 13 nematodes were identified as larval *P. decipiens*. Morphometric measurements (millimetres) of three of the worms are as follows: length, 2.688, 3.648, 4.480; preventriculus, 0.404, 0.419, 0.568; ventriculus, 0.189, 0.279, 0.358; intestinal caecum, 0.080, 0.045, 0.054; nerve ring, 0.154, 0.179, 0.144; tail, 0.092, 0.112, 0.128.

The remaining nematodes belonged to two species: *Paracuaria adunca* and *Cosmocephalus obvelatus* (Spirurida: Acuarioidea). Mean morphometric measurements and ranges of seven *P. adunca* are as follows: length, 2.178 (1.594–2.624); buccal cavity, 0.086 (0.058–0.099); nerve ring, 0.102 (0.083–0.109); excretory pore, 0.139 (0.115–0.157); esophagus, 0.301 (0.250–0.369); tail, 0.076 (0.066–0.083). Morphometric measurements of two *C. obvelatus* are as follows: length, 1.765, 1.888; buccal cavity, 0.083, 0.071; nerve ring, 0.096, 0.096; excretory pore, 0.148, 0.144; esophagus, 0.193, 0.193; tail, 0.080, 0.093.

No nematodes were found in amphipods caught in ponds from Sable Island (Table 1). However, 3.8 and 0.7% of *G. oceanicus* collected in August and December 1989, respectively, were infected with an unidentified metacercaria, probably a microphallid trematode. Three metacercariae of a different type were found in a single individual (0.2% prevalence) in August 1990.

Discussion

This is the first record of *P. decipiens* from the mysid *N. americana*. Previous natural intermediate invertebrate hosts discovered to date include the mysids *Mysis* and *Erythrops* spp. (Scott and Black 1960), the polychaete *Lepidonotus squamatus* (Val'ter and Popova 1974), and the amphipods *Caprella septentrionalis* (Val'ter 1978), *Marinogammarus obtusatus* (Val'ter 1987), *Gammarus lawrencianus*, and *Unciola irrorata* (McClelland 1990). Rates of infection are low (four worms in 3950 mysids) but comparable with previous results. McClelland (1990) found three sealworm larvae in 2000 *G. lawrencianus* and one from 500 *U. irrorata*.

Neomysis americana is one of the commonest shallow-water mysids between Virginia and the Gulf of St. Lawrence. This mysid is also the major diet item of windowpane (*Scophthalmus aquosus*) (Langton and Bowman 1981), and mysids in general are important prey items for small cod (Langton and Bowman 1980; Waiwood and Majkowski 1984). Both small cod and windowpane are frequently infected with sealworm in the vicinity of Sable Island Bank (McClelland et al. 1990); thus, mysids, and *N. americana* in particular, may be important invertebrate hosts for *P. decipiens*.

Morphometric measurements correspond to those for third-stage larval sealworm found in other macroinvertebrates (McClelland 1990). All *P. decipiens* possessed lips, boring tooth, excretory pore in the head region, mucron, intestinal caecum, and caecal ligament. Morphologically, the nematodes appear to be in the L_3 stage.

Paracuaria adunca and *C. obvelatus* are parasitic as adults in many families of fish-eating birds throughout the world (Anderson and Wong 1981; Wong and Anderson 1982a). Both nematodes are common in herring gulls (*Larus argentatus*), which commonly breed on Sable Island. Amphipods have proven to be suitable intermediate hosts for both nematodes in the laboratory (Anderson and Wong 1982; Wong and Anderson 1982b); however, neither parasite has been reported previously from a mysid. Furthermore, this is the first record of either of these worms in brackish or marine intermediate hosts, although Wong and Anderson (1982b) suggested that *C. obvelatus* could complete its life cycle in a marine environment.

Structure of the head region of both spirurid nematodes corresponds to descriptions of the L_3 stage presented in Anderson and Wong (1982) and Wong and Anderson (1982b), who studied the development of the two parasites in freshwater systems.

TABLE 1. Summary of parasites found in invertebrates collected from ponds on Sable Island.

Date	Species	Site	*n*	Method	Parasites
8/89	*Gammarus oceanicus*	Wallace Lake	1013	Microscope	39 metacercariae
12/89	*Gammarus oceanicus*	Wallace lake	741	Microscope	5 metacercariae
8/90	*Gammarus oceanicus*	Wallace lake	374	Microscope	3 metacercariae
8/90	*Gammarus oceanicus*	Pond	60	Microscope	—
8/90	*Gammarus oceanicus*	Middle Wallace	176	Microscope	—
8/90	*Neomysis americana*	Pond	796	Microscope	—
8/90	*Neomysis americana*	Middle Wallace	666	Microscope	—
8/90	*Neomysis americana*	Wallace Lake	950	Digestion	1 sealworm 2 spirurids
8/90	*Neomysis americana*	Pond	1000	Digestion	—
8/90	*Neomysis americana*	Middle Wallace	2000	Digestion	3 sealworms 7 spirurids

Paracuaria adunca possessed prominent pseudolabia, triangular in shape, and two pairs of cephalic papillae. *Cosmocephalus obvelatus* possessed two triangular pseudolabia, and cuticular grooves surrounding four prominent submedian papillae. However, morphometric measurements corresponded in general to those of large L_2 stages (Anderson and Wong 1982; Wong and Anderson 1982b), with the exception of the esophagus, which was greatly reduced in length in the Sable Island specimens. The cause of the discrepancy is unclear, but it is possible that development in brackish conditions results in both differential development and retardation of growth, when compared with development in freshwater systems. Despite this difference, the ability of these acuarioid nematodes to complete their life cycles in freshwater and brackish or marine conditions undoubtedly contributes to their widespread distribution.

Curiously, no nematodes were found in amphipods or mysids examined microscopically. Hence, microscopic examination may be less efficient than digestion for finding small nematode larvae. Thus, it is premature to conclude that mysids are more important than amphipods as intermediate hosts of these nematodes. The lakes and ponds on Sable Island, however, present an interesting opportunity to study transmission dynamics of some marine parasites, particularly sealworm, in closed systems, relatively free of many confounding variables characteristic of the open ocean.

Acknowledgements

Dr. David Sinclair and Johanne Guerin assisted with collection, examination, and digestion of invertebrates in August 1990. Dr. Don Bowen provided the opportunity to study the ponds on Sable Island. Brian Beck kindly collected the August 1989 samples and supplied and maintained the ATV's for transportation around Sable Island in December 1989 and August 1990. Ms. P. L. Wong graciously identified the acuarioid nematodes. Constructive comments by Drs. Richard Arthur and Gary McClelland substantially improved the manuscript.

References

Anderson, R. C., and P. L. Wong. 1981. Redescription of *Cosmocephalus obvelatus* (Creplin, 1825) (Nematoda: Acuarioidea) from *Larus delawarensis* Ord (Laridae). Can. J. Zool. 59: 1897–1902.

1982. The transmission and development of *Paracuaria adunca* (Creplin, 1846) (Nematoda: Acuarioidea) of gulls (Laridae). Can. J. Zool. 60: 3092–3104.

Bowen, W. D. [ed.] 1990. Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222: 306 p.

Burt, M. D. B., J. D. Campbell, C. G. Likely, and J. W. Smith. 1990. Serial passage of larval *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) in fish. Can. J. Fish. Aquat. Sci. 47: 693–695.

Langton, R. W., and R. E. Bowman. 1980. Food of fifteen Northwest Atlantic gadiform fishes. NOAA Tech. Rep. NMFS SSRF-740: iv + 24 p.

1981. Food of eight Northwest Atlantic pleuronectiform fishes. NOAA Tech. Rep. NMFS-749: iii + 16 p.

Malouf, A. H. 1986. Report of the Royal Commission on seals and sealing in Canada. Vol. 3. Ottawa, Ont. 679 p.

McClelland, G. 1990. Larval sealworm (*Pseudoterranova decipiens*) infections in benthic macrofauna, p. 47–65. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222: 306 p.

McClelland, G., R. K. Misra, and D. J. Marcogliese. 1983a. Variations in abundance of larval anisakines, sealworm (*Phocanema decipiens*) and related species in cod and flatfish from the southern Gulf of St. Lawrence (4T) and the Breton Shelf (4Vn). Can. Tech. Rep. Fish. Aquat. Sci. 1201: ix + 51 p.

1983b. Variations in abundance of larval anisakines, sealworm (*Phocanema decipiens*) and related species in Scotian Shelf (4Vs and 4W) cod and flatfish. Can. Tech. Rep. Fish. Aquat. Sci. 1202: ix + 27 p.

McClelland, G., R. K. Misra, and D. J. Martell. 1985. Variations in abundance of larval anisakines, sealworm (*Pseudoterranova decipiens*) and related species, in eastern Canadian cod and flatfish. Can. Tech. Rep. Fish. Aquat. Sci. 1392: xi + 57 p.

1987. Temporal and geographical variations in abundance of larval sealworm, *Pseudoterranova (Phocanema) decipiens* in the fillets of American plaice (*Hippoglossoides platessoides*) in eastern Canada: 1985–86 surveys. Can. Tech. Rep. Fish. Aquat. Sci. 1513: ix + 15 p.

1990. Larval anisakine nematodes in various fish species from Sable Island Bank and vicinity, p. 83–118. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222: 306 p.

Scott, D. M. 1954. Experimental infection of Atlantic cod with a larval marine nematode from smelt. J. Fish. Res. Board Can. 11: 894–900.

Scott, D. M., and W. F. Black. 1960. Studies on the life-history of the ascarid *Porrocaecum decipiens* in the Bras d'Or Lakes, Nova Scotia, Canada. J. Fish. Res. Board Can. 17: 763–774.

Scott, D. M., and H. D. Fisher. 1958. Incidence of the ascarid *Porrocaecum decipiens* in the stomachs of three species of seals along the southern Canadian Atlantic mainland. J. Fish. Res. Board Can. 15: 495–516.

Val'ter, E. D. 1978. An occurrence of *Terranova decipiens* (Nematoda, Ascaridata) in the amphipod *Caprella septentrionalis* Kroeyer. Vest. Mosk. Univ. Biol. 33: 12–14.

1987. *Marinogammarus obtusatus* (Amphipoda), a new intermediate host of the nematode *Pseudoterranova decipiens*. Nauchn. Dokl. Vyssh. Shk. Biol. Nauki 6: 28–32. (Can. Transl. Fish. Aquat. Sci. 5419)

Val'ter, E. D., and T. I. Popova. 1974. The role of the polychaete *Lepidonotus squamatus* (L.) in the biology of anisakids. Tr. Belomorsk. Biol. Stn. Mosk. Gos. Univ. 4: 177–182. (Fish. Mar. Serv. Transl. Ser. 3604)

Waiwood, K., and J. Majkowski. 1984. Food consumption and diet composition of cod, *Gadus morhua*, inhabiting the southwestern Gulf of St. Lawrence. Environ. Biol. Fishes 11: 63–78.

Wong, P. L., and R. C. Anderson. 1982a. Redescription of *Paracuaria adunca* (Creplin, 1846) (Nematoda: Acuarioidea) from *Larus delawarensis* Ord (Laridae). Can. J. Zool. 60: 175–179.

1982b. The transmission and development of *Cosmocephalus obvelatus* (Nematoda: Acuarioidea) of gulls (Laridae). Can. J. Zool. 60: 1426–1440.

Antifreeze Production, Freeze Resistance, and Overwintering of Juvenile Northern Atlantic Cod (*Gadus morhua*)

Sally V. Goddard, Ming H. Kao, and Garth L. Fletcher

Marine Sciences Research Laboratory, Ocean Sciences Centre and Department of Biology, Memorial University of Newfoundland, St. John's, Nfld. A1C 5S7, Canada

Goddard, S. V., M. H. Kao, and G. L. Fletcher. 1992. Antifreeze production, freeze resistance, and overwintering of juvenile northern Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 49: 516–522.

Four size groups of northern Atlantic cod (*Gadus morhua*) (juveniles <15, 15–25, and 26–40 cm and adults >50 cm) were investigated over a winter cycle for their ability to increase freeze resistance by producing plasma antifreeze glycoproteins. All juveniles had significantly higher plasma antifreeze levels than adults during the winter (January–March) under similar conditions of cycling temperature and ambient photoperiod. Highest winter plasma antifreeze levels and lowest plasma freezing temperatures were consistently found in the 15–25 cm group. Fish length and plasma antifreeze levels were inversely related from January to April, with the exception of the 0+ cod. All juvenile groups developed considerable freeze protection early in the winter cycle before the onset of freezing temperatures. However, the adults were not significantly protected until the end of January, when ambient temperatures had fallen below 0°C. The 15–25 cm cod were held in three cycling temperature regimes. Induction temperatures for antifreeze production in this size group appeared to be between 2 and 3°C, as compared with between 1 and 0°C for the adults. We suggest that these patterns of antifreeze production may have direct bearing on habitat selection and overwintering behaviour of the northern Atlantic cod at different stages of development.

On a tenté de déterminer, au cours d'un hiver, la capacité de quatre groupes de taille de la morue franche (*Gadus morhua*) (soit des juvéniles de moins de 15 cm, de 15 à 25 cm et de 26 à 40 cm et des adultes de plus de 50 cm) d'augmenter leur résistance au gel en produisant des glycoprotéines antigel du plasma. Tous les juvéniles présentaient des teneurs nettement plus élevées en protéines antigel du plasma que les adultes pendant l'hiver (janvier–mars) dans des conditions semblables de température cyclique et de photopériode ambiante. Le groupe de juvéniles de 15 à 25 cm de longueur présentait régulièrement les teneurs les plus élevées d'antigel et les températures les plus basses de gel du plasma. Sauf dans le cas des morues de moins d'un an, la longueur du poisson et les teneurs en antigel du plasma étaient en corrélation inverse de janvier à avril. Tous les groupes de juvéniles ont développé une forte capacité de résistance au gel dès le début de l'hiver avant le point de gel. Toutefois, les adultes n'étaient pas protégés de façon significative jusqu'à la fin de janvier, lorsque les températures ambiantes avaient chuté au-dessous de 0°C. La température de stimulation de la production d'antigel chez les juvéniles de 15 à 25 cm de longueur exposés à trois régimes de température cyclique semblait varier entre 2 et 3°C, par rapport à entre 1 et 0°C chez les adultes. Selon les auteurs, ces régimes de production d'antigel peuvent avoir une incidence directe sur le choix de l'habitat et le comportement hivernal de la morue franche de l'Atlantique nord à différents stades de développement.

Received May 21, 1991
Accepted October 4, 1991
(JB044)

Reçu le 21 mai 1991
Accepté le 4 octobre 1991

Most teleost fish inhabiting temperate marine waters have plasma freezing temperatures of between −0.5 and −0.8°C (Holmes and Donaldson 1969). Fish encountering water temperatures lower than their plasma freezing point face the risk of freezing. The danger becomes acute if ice crystals are present in the water column, since these will seed the formation of ice within the body fluids of supercooled fish. In the polar and subpolar oceans, seawater temperatures of between −1 and −2°C are not unusual, and fish living in such potentially dangerous environments have, of necessity, developed certain behavioural and/or physiological strategies to avoid injury or death by freezing (G. L. Fletcher, R. A. Myers, S. A. Akenhead, and P. L. Davies, unpubl. data).

Some teleost fish living in subpolar regions avoid freezing winter conditions by migrating, either into warmer areas of oceanic water (Reddin and Shearer 1987) or upstream into bodies of freshwater (Dempson and Kristofferson 1987). In both the Arctic and Antarctic oceans, teleost fish can be found living in a permanently supercooled state at depths sufficient to preclude any contact with ice crystals (Scholander et al. 1957; Leivestad 1965; DeVries 1970).

However, many teleost fish inhabiting the polar, subpolar, and temperate oceans are being found to have the ability to produce protein macromolecules that act as antifreezes. These antifreeze polypeptides (AFP) or antifreeze glycopeptides (AFGP) are diverse in structure (Davies and Hew 1990; Davies et al. 1988) and are primarily produced in the liver, from whence they are distributed throughout the plasma and extracellular fluids. They act noncolligatively to lower the freezing point whilst having no effect on the melting point of the body fluids (DeVries 1983).

Permanently elevated levels of AFP or AFGP can be found in fish inhabiting waters which pose a year-round threat of freezing (DeVries 1980). Fish living at lower latitudes (in subpolar or temperate seas) may exhibit fluctuating levels of AFP or AFGP, with peak levels developing during the winter. This is the pattern of antifreeze production found in the Atlantic cod (*Gadus morhua*). During the summer months, the plasma freezing point of adult cod is between −0.7 and −0.8°C, falling to below −1.1°C in February–April (Fletcher et al. 1987). This increase in freezing resistance is largely due to the appearance of AFGP in the plasma of the adults when they are exposed to 0°C water (Fletcher et al. 1987; Hew et al. 1981).

In the Northwest Atlantic, cod are found from Frobisher Bay (approximate latitude 63°N) to Cape Hatteras (approximate latitude 35°N) and, depending on the season, at depths ranging from about 5 m in the inshore areas in summer to water as deep as 600 m on the edge of the continental shelf in winter (Jackson 1988). In the Newfoundland region (NAFO Divisions 2J, 3K, and 3L), adult cod undergo an annual cycle of inshore–offshore migrations (Templeman 1979; Lear and Green 1984; Pinhorn 1984), overwintering along the outer slopes of the continental shelf at depths of 200–600 m. With increasing depth, the likelihood of encountering ice in the water column is reduced. Therefore in the adult cod, the need for increased freeze protection may be infrequent or sporadic (Fletcher et al., unpubl. data).

While the summer locations of juvenile cod are well documented, there are few reports on the winter habitats of young cod from their first year of life until they are recruited into the fishery. Templeman and Fleming (1965) reported the winter occurrence of numerous small (<30 cm) cod in St. Mary's Bay, Newfoundland, water temperatures at this time reaching −1.4°C. Brown et al. (1989) demonstrated that 0+ cod have the capacity for continued and efficient growth at low water temperatures and suggested that juvenile (0+) cod may remain in the cold coastal regions of Newfoundland over winter because of high food supply and/or lower predation pressure. If the juveniles overwinter in areas that present a potentially greater danger of freezing than that experienced by the adults, it might be expected that they would have a greater capacity for the development of freeze resistance.

Kao and Fletcher (1988) established that juvenile cod (mean length 33 cm, mean age 3 yr) can be more freeze resistant than adults (>45 cm). Adult and juvenile cod were kept under the same winter conditions and by March 1987, juvenile cod had a mean plasma freezing temperature of −1.55°C and mean thermal hysteresis value of 0.625°C as compared with −1.23 and 0.375°C, respectively, for the adults. Thermal hysteresis, the difference between the freezing and melting temperature of a sample, is used as a direct measure of antifreeze levels.

In the present study, the ability of juvenile (0+ to 3+) and adult cod to protect themselves from freezing by the synthesis of AFGP was further investigated, and the results are related to possible overwintering behaviour patterns of juvenile cod in the wild.

Materials and Methods

During July and August of 1986–87, cod were caught in cod traps by local fishers in Conception Bay and transported to the Marine Science Research Laboratories, Logy Bay. Experimental animals were initially maintained in a 40 000-L seawater (32‰) aquarium under seasonally ambient conditions of temperature and photoperiod. All animals were fed twice a week on capelin (*Mallotus villosus*). During the same period, juvenile cod (<10 cm) were caught by seining from Bellevue Beach, Trinity Bay. These small fish were also fed on capelin and maintained in aquaria under seasonally ambient conditions of temperature and photoperiod prior to experimentation (Fletcher 1977).

In all size groups of animals, blood samples were taken from a caudal blood vessel using plastic 3-cm^3 syringes, fitted with 21-gauge needles when sampling cod >40 cm long and 25-gauge needles for cod <40 cm in length. Blood sampling took less than 1 min, and no anaesthetic was used. Samples were placed in Vacutainers containing sodium heparin (Becton Dickinson), and the cells were then separated from the plasma by centrifugation for 10 min at 4000*g*. Plasma samples were stored frozen at −20°C until analyzed.

Plasma freezing and melting points were determined using a nanolitre osmometer (Clifton Technical Physics, Hartford, New York). Using this technique, the melting and freezing behaviour of a single ice crystal is observed under a microscope. Characteristically, AFP and AFGP lower the plasma freezing point while having no influence on the melting point. The difference between the freezing and melting temperature of a sample is termed the thermal hysteresis, and this is used as a direct measure of antifreeze activity (Kao et al. 1986).

Water temperatures were measured several times a week using a mercury thermometer calibrated to 0.1°C.

Two main experiments on the response of different size groups of cod to winter temperature cycles were carried out during the winter of 1987–88, and additional data were obtained during the winter of 1986–87. Groups were compared using Student's *t*-test, one-way ANOVA, and Duncan's multiple range test.

Experiment 1. Antifreeze Production and Freeze Resistance in Four Size Groups of Cod over a Winter Temperature Cycle (1987–88)

Cod were divided into four size groups on the basis of length (snout to midfork of the tail) and were kept in three tanks in the same outbuilding under essentially identical conditions of temperature and photoperiod. Groups were separated to avoid predation of the smaller fish by the adults. Size groups were as follows: <15 cm (age 0+ to 1+), 15–25 cm (age 1+ to 2+), 26–40 cm (age 2+ to 3+), and >50 cm (mature adults >5 yr) (age at length from Fleming 1960; Jackson 1988). The two smallest size groups were placed in 300 L tanks on their arrival at the laboratory and were sampled directly from those tanks, while the 26–40 and >50 cm cod were maintained in a 40 000 L seawater tank throughout the experiment. Blood samples were taken from a number of fish (Table 1) from each group on a monthly basis (November–June, omitting March). All fish were fed twice weekly.

Experiment 2. Effects of Temperature on Plasma Antifreeze Levels in 15–25 cm Cod over One Winter (1987–88)

Three groups of 15–25 cm cod were maintained in tanks designated as A, B, and C and were exposed to seasonally ambient photoperiod. The tank A group in experiment 2 is the same 15–25 cm group described in experiment 1 (above). Temperatures in tank A were consistently lower than those in tanks B and C: group A fish experienced subzero temperatures by the beginning of January and a minimum of −1.5°C by the end of February. The temperature in tank B did not reach zero until February, while in tank C the temperatures fell below 0.5°C on only 8 d out of the whole winter cycle. A number of fish from each of the three groups were sampled at monthly intervals from November to June (omitting March) (see Table 3 for values of *n*). All fish were fed twice weekly.

In the light of the above experiments, data collected over the winter of 1986–87 on thermal hysteresis levels in three size groups of cod (<15, 26–40, and >50 cm) were reexamined. From December to March 1986–87, two groups of cod (>50 and 26–40 cm) were kept together in a 40 000-L seawater tank

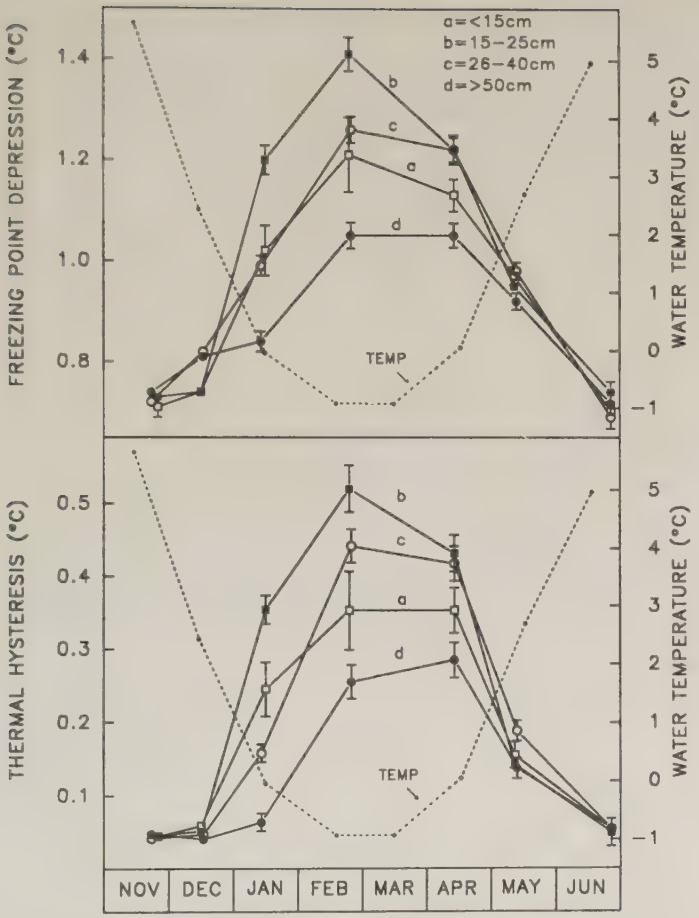


FIG. 1. Seasonal changes in the plasma freezing point depression and thermal hysteresis in four size groups of cod (<15, 15–25, 26–40, and >50 cm). Values of thermal hysteresis and plasma freezing point depression are plotted as means ± 1 SE. Temperatures are the monthly means of values recorded several times each week from November to June 1987–88.

at ambient temperature and photoperiod. In addition, 0+ cod (<15 cm) that had been obtained by seining from Bellevue Beach, Newfoundland, were maintained in the tank designated tank B (described above, experiment 2) at ambient photoperiod and at temperatures slightly higher than those experienced by the 26–40 and >50 cm groups (see Fig. 4). Fish were fed twice weekly and were sampled as follows: <15 cm fish, January 21 and March 4, 1987; >50 cm fish, December 17, 1986, January 9, 1987, and March 4, 1987; 26–40 cm fish, March 4, 1987, only. Thermal hysteresis levels were determined for these samples, and the results were compared with the data for 1987–88. March 4, 1987, data for 26–40 and >50 cm cod have been published by Kao and Fletcher (1988).

Results

Experiment 1. Effects of Fish Size on AFGP Production

In November and December, all groups were at or near the baseline thermal hysteresis level of 0.045 ± 0.01°C (the limit of accuracy of the osmometer). There were no significant differences between the groups, and it was assumed that little or no AFGP were present in the plasma (Fig. 1). By January, the adult fish had produced little antifreeze, and thermal hysteresis values had hardly changed from the baseline level; however, all three groups of juvenile fish had produced significant quantities of antifreeze (Fig. 1; Table 1). Using the data presented in Fig. 1, levels of thermal hysteresis were estimated for all four groups on the day that the temperature of their surroundings first reached 0°C. Similarly, estimates were made of the dates by which each group had developed a thermal hysteresis level of 0.15°C. These estimated values (Table 2) indicate that all juvenile groups were making AFGP earlier in the winter and at higher temperatures than were the adults. Of the three juvenile groups studied, the 15–25 cm cod were the most temporally advanced in the production of antifreeze. They were followed by the <15 cm group and then the 26–40 cm group (Fig. 1). In January, antifreeze levels produced by all four groups were significantly different from each other (Fig. 1; Table 1), and highest AFGP levels were recorded in the 15–25 cm group.

By February, when water temperatures were consistently below −1°C, all size groups had developed considerable levels of thermal hysteresis. The 15–25 cm group developed the highest levels of antifreeze and the greatest tolerance to cold water as measured by the plasma freezing temperature. The 26–40 cm cod had overtaken the <15 cm group in the production of AFGP and were more freeze resistant. All juvenile groups had significantly higher thermal hysteresis levels and significantly lower plasma freezing points than the adults (Fig. 1; Table 1).

In April, AFGP levels were declining in all the juvenile groups. In the absence of a March value, it cannot be stated categorically that levels of plasma AFGP were falling in the adults, but it seems most likely that this was the case. In all groups, antifreeze levels continued to decline during May, and by June, all groups were back at baseline levels of thermal hysteresis and plasma freezing temperature.

Experiment 2. Effects of Temperature on AFGP Production in 15–25 cm cod

By January, cod in all three temperature regimes had built up considerable quantities of AFGP as measured by thermal hysteresis (Fig. 2; Table 3). There was no significant difference between thermal hysteresis levels in tanks A and B for the entire course of the experiment (see Table 3 for Duncan's groupings), and this was also the case for plasma freezing temperatures. Although in January the levels of antifreeze produced by the cod in tank C lagged somewhat behind those in tanks A and B, by February there was no significant difference between the three groups. Mean tank temperatures (degrees Celsius) for January were A = −0.07, B = 0.81, and C = 1.32 and for February were A = −0.92, B = −0.01, and C = 0.58. Values of thermal hysteresis for the fish in tanks A, B, and C, recorded between November and February (rising phase of AFGP production), were plotted against temperature (Fig. 3) where temperatures are the means of values recorded for 5 d prior to each actual sampling date. Thermal hysteresis values for November and December (Fig. 2) gave a baseline of 0.048°C.

In April, thermal hysteresis values for the fish in tank C were significantly lower than those in tanks A and B (Fig. 2). Levels of AFGP were falling in all fish by April. It seems likely, therefore, that AFGP synthesis had ceased and that the more rapid drop in thermal hysteresis levels in tank C was due to higher AFGP clearance rates at higher temperatures (Fletcher et al. 1987).

The results of the experiment on three size groups carried out over the winter of 1986–87 (Fig. 4) appeared to support those of experiment 1, namely that while both juvenile groups

TABLE 1. Plasma freezing temperatures and thermal hysteresis (antifreeze activity) in four size groups of cod, January – April 1988. All values are presented as means ± 1 SE. Numbers of fish (n) are given in parentheses. Within each month, comparisons between groups were carried out by a one-way analysis of variance followed by Duncan's multiple range test, and groups followed by a different uppercase letter differed significantly ($P < 0.001$). Differences between groups were calculated at the 0.05 level.

	Fish length (cm)			
	<15	15–25	26–40	>50
Plasma freezing temperature (°C)				
Jan.	−1.02 ± 0.04 (5) B	−1.20 ± 0.05 (8) A	−0.99 ± 0.03 (18) B	−0.84 ± 0.02 (12) C
Feb.	−1.21 ± 0.03 (8) B	−1.41 ± 0.07 (5) A	−1.26 ± 0.03 (17) B	−1.05 ± 0.03 (18) C
Apr.	−1.13 ± 0.05 (9) AB	−1.22 ± 0.03 (7) A	−1.22 ± 0.03 (16) A	−1.05 ± 0.02 (21) B
Thermal hysteresis (°C)				
Jan.	0.246 ± 0.033 (5) B	0.354 ± 0.037 (8) A	0.158 ± 0.02 (18) C	0.064 ± 0.012 (12) D
Feb.	0.353 ± 0.031 (8) BC[a]	0.524 ± 0.054 (5) A	0.442 ± 0.032 (17) AB	0.255 ± 0.023 (18) C[a]
Apr.	0.353 ± 0.048 (9) AB	0.432 ± 0.031 (7) A	0.418 ± 0.025 (16) A	0.285 ± 0.024 (21) B

[a] Using a t-test, February values of thermal hysteresis for <15 and >50 cm fish were significantly different ($P = 0.025$).

TABLE 2. Timing and levels of antifreeze buildup as measured by thermal hysteresis (°C) in four size groups of cod, winter 1987–88.

	Fish length (cm)			
	<15	15–25	26–40	>50
Thermal hysteresis on day 1 at 0°C (Jan. 7, 1988)	0.196	0.273	0.133	0.057
Thermal hysteresis of 0.15°C (rising phase only)	Dec. 31	Dec. 26	Jan. 11	Feb. 1

developed higher levels of thermal hysteresis than the adults, by March the <15 cm group was not as freeze resistant as the larger juveniles. However, the <15 cm group experienced slightly warmer temperatures than the larger size groups from December to March. This may have had some effect on the concentrations of AFGP built up by the <15 cm fish and should be considered when making comparisons between the two juvenile groups. Analysis of the March 4, 1987, data showed that while the two juvenile groups were similar, both groups were significantly different from the adults (Table 4).

Discussion

The results of this investigation show that juvenile northern Atlantic cod are capable of developing higher plasma concentrations of antifreeze, earlier in the winter, than are the adults. The level of freeze resistance developed in fish has been shown to be proportional to the concentration of antifreeze present in the plasma and extracellular fluids (Kao et al. 1986; Fletcher et al. 1986). Our data indicate that small cod are capable of surviving harsher winter conditions than are the adults, and we suggest that this may influence their overwintering behaviour.

Previous work has shown that 0°C temperatures are necessary for the buildup of plasma AFGP in the adult cod (Fletcher et al. 1987) and that photoperiod appears to play little part in the onset of cod antifreeze production. In addition, winter plasma antifreeze levels in adult cod are usually insufficient to protect them from freezing should they encounter temperatures lower than −1.2°C in the presence of ice crystals.

This lack of advance preparation for icy conditions is probably compensated for by the migratory behaviour of adult cod, which move offshore late in the year to overwinter in deeper, more protected waters. In contrast, winter flounder (*Pseudopleuronectes americanus*), which remain in relatively shallow, potentially ice-laden waters over the winter, start to produce antifreeze in November, and production is stimulated primarily by photoperiod (Fletcher et al. 1989). With the arrival of short daylengths, the release from the pituitary of antifreeze-inhibiting factor, now shown to be growth hormone (Idler et al. 1989), is itself inhibited by the central nervous system (Fletcher et al. 1984), and antifreeze is produced. This ensures that the winter flounder is adequately protected from freezing, well in advance of the arrival of freezing conditions in the inshore waters it inhabits.

The overwintering locations of juvenile cod (0+ to 3+) of the Northern cod stock have not, as yet, been clearly defined. However, the results of this investigation into the pattern of juvenile antifreeze production extend the findings of Kao and Fletcher (1988) and suggest that juvenile cod are capable of surviving in the coastal areas of Newfoundland over winter. In January and February, all the juvenile groups examined in our experiments had levels of antifreeze (as measured by thermal hysteresis) significantly higher than those of the adults. Also, all juvenile groups started producing measurable quantities of antifreeze earlier in the winter than did the adults (Table 2). These results suggest that not only are the juveniles able to withstand lower temperatures in the presence of ice over winter, but also that they are physiologically prepared to meet these temperatures by the induction and buildup of plasma AFGP at higher temperatures and earlier in the winter cycle than the adults. Results from experiment 2 suggest an induction temperature above 2°C for 15–25 cm cod, as compared with between 1 and 0°C for the adults (Fletcher et al. 1987). There was no significant difference in the maximum (February) levels

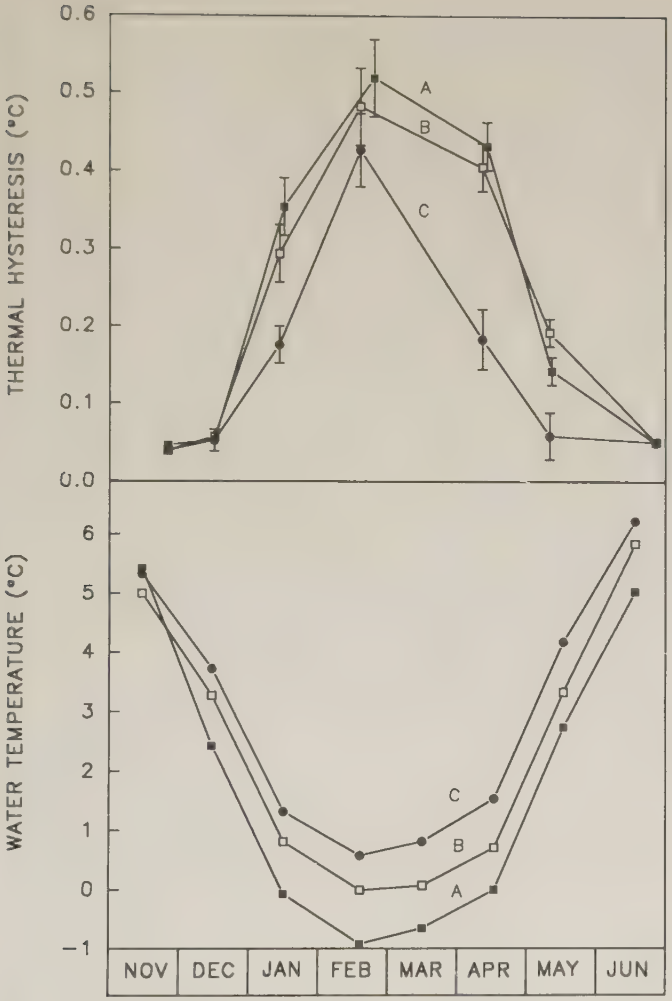


FIG. 2. Effect of water temperature on the seasonal cycle of antifreeze production, as measured by plasma thermal hysteresis, in 15–25 cm cod in three temperature regimes (A, B, and C). Thermal hysteresis values are plotted as means ± 1 SE. Water temperatures in tanks A, B, and C are the means of values recorded several times each week from November to June 1987–88.

TABLE 3. Plasma thermal hysteresis levels (°C) for 15–25 cm cod in three temperature regimes, January–May 1988. Values are presented as means ± 1 SE. Probability values for each month are given in column 5. See legend of Table 1 for further explanation.

	Tank A	Tank B	Tank C	*P*
Jan.	0.354 ± 0.037 (8) A	0.294 ± 0.024 (6) A	0 176 ± 0.036 (5) B	<0.01
Feb.	0.524 ± 0.05 (5) A	0.483 ± 0.047 (5) A	0.427 ± 0.015 (5) A	0.299
Apr.	0.432 ± 0.031 (7) A	0.405 ± 0.039 (10) A	0.183 ± 0.026 (9) B	<0.001
May	0.142 ± 0.018 (6) A	0.202 ± 0.032 (8) A	0.058 ± 0.005 (8) B	<0.001

of antifreeze built up by the 15–25 cm cod in three temperature regimes in experiment 2. This suggests that even in a comparatively mild winter, juvenile cod can produce quantities of antifreeze sufficient to confer protection should harsher conditions arrive.

There is some evidence to suggest that in some cases, juvenile Northern cod overwinter in inshore areas. Templeman and Fleming (1965) described a population of small cod, mostly 14–21 cm long, that spent the winter, from February to April, in St. Mary's Bay, Newfoundland. Temperatures during this time were consistently below −1.3°C. In April, of a total of 693 fish observed, 612 were 11–20 cm and 62 were 21–30 cm in length. These juvenile cod were feeding actively on a diet consisting primarily of euphausids and amphipods.

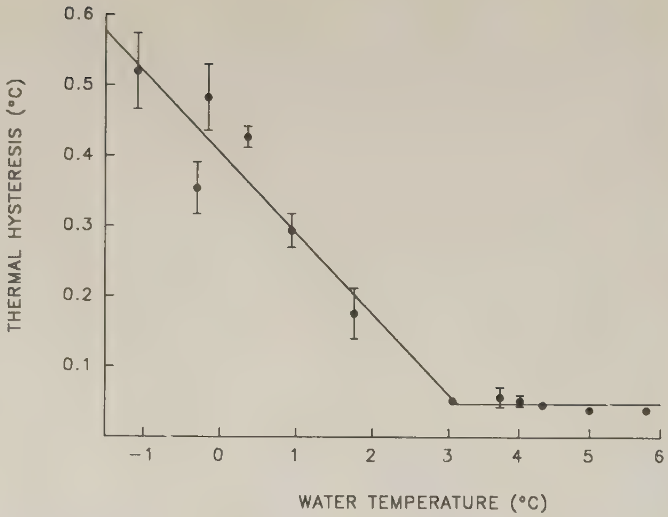


FIG. 3. Thermal hysteresis levels in three groups of 15–25 cm cod (tanks A, B, and C) plotted against water temperature. Thermal hysteresis values are plotted as means ± 1 SE. Only those values of thermal hysteresis from November to February (rising phase of production) are included. Mean baseline level = 0.045°C thermal hysteresis. Regression analysis was carried out on all individual values of thermal hysteresis above 0.1°C (January and February data). Water temperatures are the means of tank temperatures recorded for 5 d prior to the sampling date.

In a series of winter tows in the Gulf of St. Lawrence (1957–62), Jean (1964) found cod of 10–13 cm in water <30 m deep and at temperatures as low as −1.5°C. Cod of 14–22 cm were reported at depths of 35–120 m in temperatures of −1.0°C. With increasing depth, larger size groups of cod were found. The maximum length of cod found within the Gulf was 39 cm. It was reported that cod larger than 39 cm had joined the adult stock overwintering outside the Gulf in areas off the Atlantic coast of Nova Scotia. A similar situation has been described for the Arcto-Norwegian cod stocks, where large immatures migrate with the adults (Trout 1957), while small cod (up to age group 2+) can be found in the Spitzbergen area prior to joining the adults in their southerly migrations (Iversen 1934; Hansen 1949). Bathymetric separation of size groups is well documented for gadoids in general and cod in particular (Templeman 1966; Tremblay and Sinclair 1985; Methven and McKelvie 1986; Iversen 1932; Stevenson Macdonald et al. 1984), and since adult cod will prey on juveniles if they are available (Postolaky 1972; Keats et al. 1987), this tactic of overwintering in cold shallow water may be of great survival value to the smaller juveniles. It has been shown experimentally that cod are able to distinguish a 0.05°C change in temperature (Bull 1936, 1951). This sensitivity to changes in the thermal characteristics of their surroundings suggests that while overwintering offshore, adult cod would be able to detect and, in general, avoid very cold water. They may, therefore, only rarely come into contact with subzero temperatures, for example as a result of feeding forays into bodies of cold water (Graham et al. 1954).

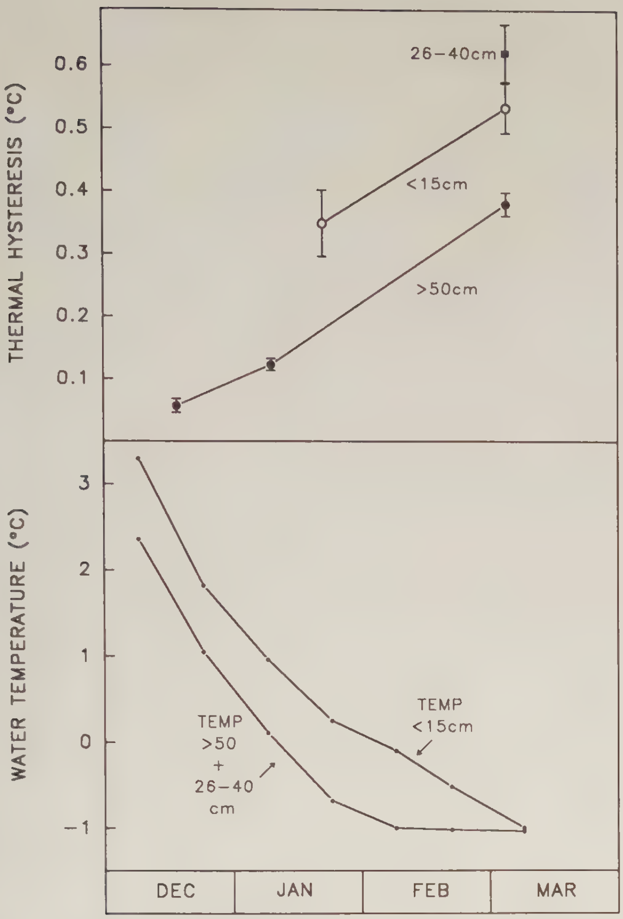


FIG. 4. Thermal hysteresis levels in three size groups of cod (<15, 26–40, and >50 cm) built up over the winter of 1986–87. Values of thermal hysteresis are expressed as means ± 1 SE. Water temperatures to which the three size groups were exposed (lower graph) are plotted as semimonthly means of values recorded several times each week during December–March 1986–87.

TABLE 4. Plasma thermal hysteresis levels (°C) in three size groups of cod, March 1987. Values are presented as means ± 1 SE. See legend of Table 1 for further explanation.

Fish length (cm)		
<15	26–40	>50
0.535 ± 0.04 (11) A	0.622 ± 0.05 (13) A	0.387 ± 0.02 (24) B

Together, these factors suggest that juvenile cod are spatially separated from the adults over winter. The bays and inshore areas off the coast of Newfoundland are considered summer nursery grounds for cod (Lear and Green 1984). Our results suggest that since small juveniles (0+ to 2+) are physiologically prepared to survive exposure to icy, subzero waters during the winter months, they could overwinter in inshore locations. Some advantages to the small cod of overwintering inshore have already been mentioned, and provided no environmental factor (for example, a food shortage) prompts them to migrate, it seems reasonable to suggest that juvenile cod might remain in their nursery areas for the first year or two of life. During this time they would probably develop a strong sense of the characteristics and identity of their own nursery areas. This could be a factor in any subsequent onshore–offshore migrations of these individuals.

In cod longer than 15 cm, there appears to be a correlation between fish length and the timing and quantity of antifreeze production; the smaller the fish, the earlier AFGP appear in the plasma and the greater are the quantities built up during the winter. This would allow the smaller fish to remain in more shallow areas during the winter, while the older juveniles move progressively offshore until they are large enough to migrate with the adults, as described for the Gulf of St. Lawrence cod (Jean 1964). Differences in winter plasma antifreeze levels that reflect differences in the migratory behaviour of juveniles and adults have been described for the Atlantic herring (*Clupea harengus harengus*) in the Gulf of St. Lawrence (Chadwick et al. 1990). Our results suggest that this may also be the case for cod in the Newfoundland area.

As a group, however, the <15 cm 0+ fish did not conform to this hypothesis. Our 15–25 cm group was more resistant to low temperatures than the <15 cm group in January, and later in the winter, both the 15–25 and 26–40 cm groups were more freeze resistant than the <15 cm group. It is possible that these very small fish are less freeze protected than the larger juveniles, but that they avoid freezing in shallow water by employing some behavioural tactic in addition to the production of antifreeze. Some species, for example the cunner (*Tautogolabrus adspersus*), overwinter in shallow water and avoid ice contact by hiding in crevices (Valerio et al. 1990).

It is also possible that the first overwintering period is a time of great selection for cold tolerance among the very small cod. It might thus be expected that those individuals reaching their second winter would be the ones having a greater ability to withstand cold temperatures by manufacturing antifreeze. There are no reports of mass mortalities of 0+ cod during the winter or early spring; however, such an event might go unnoticed, as the fish are very small. Low temperature tolerance may be a factor of critical importance in habitat selection by 0+ cod, since their ability to produce AFGP will have a direct influence on the winter habitats available to these young fish.

Acknowledgements

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada and by the National Centres of Excellence Program (Ocean Production Enhancement Network).

References

BROWN, J. A., P. PEPIN, D. A. METHVEN, AND D. C. SOMERTON. 1989. The feeding, growth and behaviour of juvenile cod, *Gadus morhua* L., in cold environments. J. Fish Biol. 35: 373–380.

BULL, H. O. 1936. Studies on conditioned responses in fishes. Part VII. Temperature perception in teleosts. J. Mar. Biol. Assoc. U.K. 21: 1–28.

1951. An evaluation of our knowledge of fish behaviour in relation to hydrography. Rapp. Cons. Int. Explor. Mer 131: 8–23.

CHADWICK, E. M. P., D. K. CAIRNS, H. M. C. DUPUIS, K. V. EWART, M. H. KAO, AND G. L. FLETCHER. 1990. Plasma antifreeze levels reflect the migratory behaviour of Atlantic herring (*Clupea harengus harengus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 47: 1534–1536.

DAVIES, P. L., AND C. H. HEW. 1990. Biochemistry of fish antifreeze proteins. FASEB J. 4: 2460–2468.

DAVIES, P. L., C. L. HEW, AND G. L. FLETCHER. 1988. Fish antifreeze proteins: physiology and evolutionary biology. Can. J. Zool. 66: 2611–2617.

DEMPSON, J. B., AND A. H. KRISTOFFERSON. 1987. Spatial and temporal aspects of the ocean migration of anadromous Arctic char. Am. Fish. Soc. Symp. 1: 340–357.

DEVRIES, A. L. 1970. Freezing resistance in Antarctic fishes, p. 320–338. *In* M. W. Holdgate [ed.] Antarctic ecology. Vol. 1. Academic Press, New York, NY.

1980. Biological antifreezes and survival in freezing environments, p. 583–607. *In* R. Gilles [ed.] Animals and environmental fitness. Pergamon Press, Oxford and New York.

1983. Antifreeze peptides and glycopeptides in cold-water fishes. Annu. Rev. Physiol. 45: 245–260.

Fleming, A. M. 1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area, 1947–1950. J. Fish. Res. Board Can. 17: 775–809.

Fletcher, G. L. 1977. Circannual cycles of blood plasma freezing point and Na and Cl concentrations in Newfoundland winter flounder (*Pseudopleuronectes americanus*): correlation with water temperature and photoperiod. Can. J. Zool. 55: 789–795.

Fletcher, G. L., D. R. Idler, A. Vaisius, and C. L. Hew. 1989. Hormonal regulation of antifreeze protein gene expression in winter flounder. Fish Physiol. Biochem. 7: 387–393.

Fletcher, G. L., M. H. Kao, and R. M. Fourney. 1986. Antifreeze peptides confer freezing resistance to fish. Can. J. Zool. 64: 1897–1901.

Fletcher, G. L., M. J. King, and C. L. Hew. 1984. How does the brain control the pituitary's release of antifreeze synthesis inhibitor? Can. J. Zool. 62: 839–844.

Fletcher, G. L., M. J. King, and M. H. Kao. 1987. Low temperature regulation of antifreeze glycopeptide levels in Atlantic cod (*Gadus morhua*). Can. J. Zool. 65: 227–233.

Graham, M., G. C. Trout, R. J. H. Beverton, J. Corlett, A. J. Lee, and R. W. Blacker. 1954. Report on research from the Ernest Holt into the fishery near Bear Island 1949 and 1950. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Ser. II 18(3): 87 p.

Hansen, P. M. 1949. Studies on the biology of the cod in Greenland waters. Rapp. Cons. Int. Explor. Mer 123: 1–77.

Hew, C. L., D. Slaughter, G. L. Fletcher, and S. B. Joshi. 1981. Antifreeze glycoproteins in the plasma of Newfoundland Atlantic cod (*Gadus morhua*) Can. J. Zool. 59: 2186–2192.

Holmes, W. N., and E. M. Donaldson. 1969. The body compartments and distribution of electrolytes, p. 1–89. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. 1. Academic Press, New York, NY.

Idler, D. R., G. L. Fletcher, S. Belkhode, M. J. King, and S. J. Hwang. 1989. Regulation of antifreeze protein production in winter flounder: a unique function for growth hormone. Gen. Comp. Endocrinol. 74: 327–334.

Iversen, T. 1932. Some observations on fry in trawl catches in the Barents Sea. Rapp. Cons. Int. Explor. Mer 85: 3–6.

1934. Some observations on cod in Northern waters. Rep. Norw. Fish. Mar. Invest. Vol. IV, No. 8 (Bergen): 35 p.

Jackson, L. 1988. The science of cod. Considerations in the scientific study and assessment of cod stocks in the Newfoundland region. Fo'c'sle 8(2): 29 p.

Jean, Y. 1964. Seasonal distribution of cod (*Gadus morhua* L.) along the Canadian Atlantic coast in relation to water temperature. J. Fish. Res. Board Can. 21: 429–460.

Kao, M. H., and G. L. Fletcher. 1988. Juvenile Atlantic cod (*Gadus morhua*) can be more freeze resistant than adults. Can. J. Fish. Aquat. Sci. 45: 902–905.

Kao, M. H., G. L. Fletcher, N. C. Wang, and C. L. Hew. 1986. The relationship between molecular weight and antifreeze polypeptide activity in marine fish. Can. J. Zool. 64: 578–582.

Keats, D. W., D. H. Steele, and G. R. South. 1987. The role of fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua* L.) in inshore waters off eastern Newfoundland. Can. J. Zool. 65: 49–53.

Lear, W. H., and J. M. Green. 1984. Migration of the "northern" Atlantic cod and the mechanisms involved, p. 309–315. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] Mechanisms of migration in fishes. Plenum Press, New York, NY.

Leivestad, H. 1965. Supercooling and osmoregulation in teleosts of the boreal and sub-Arctic. Int. Comm. Northwest Atl. Fish. Spec. Publ. No. 6: 747–752.

Methven, D. A., and D. S. McKelvie. 1986. Distribution of *Phycis chesteri* (Pisces:Gadidae) on the Grand Bank and Labrador Shelf. Copeia 4: 886–891.

Pinhorn, A. T. 1984. Inshore exploitation of Atlantic cod, *Gadus morhua*, in Labrador and eastern Newfoundland waters. J. Northwest Atl. Fish. Sci. 5: 79–84.

Postolaky, A. I. 1972. Biology and fishing of Labrador and Newfoundland cod. Fish. Res. Board Can. Transl. Ser. 2151: 44 p.

Reddin, D. G., and W. M. Shearer. 1987. Sea surface temperature and distribution of Atlantic salmon in the Northwest Atlantic Ocean. Am. Fish. Soc. Symp. 1: 262–275.

Scholander, P. F., L. van Dam, J. W. Kanwisher, H. T. Hammel, and M. S. Gordon. 1957. Supercooling and osmoregulation in arctic fish. J. Cell. Comp. Physiol. 49: 5–24.

Stevenson Macdonald, J., M. J. Dadswell, R. G. Appy, G D. Melvin, and D. A. Methven. 1984. Fishes, fish assemblages, and their seasonal movements in the lower Bay of Fundy and Passamaquoddy Bay, Canada. Fish. Bull. 82(1): 121–139.

Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. 154: 170 p.

1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962–66. Int. Comm. Northwest Atl. Fish. Res. Bull. No. 14: 50 p.

Templeman, W., and A. M. Fleming. 1965. Cod and low temperature in St. Mary's Bay, Newfoundland. Int. Comm. Northwest Atl. Fish. Spec. Publ. No. 6: 131–135.

Tremblay, M. J., and M. Sinclair. 1985. Gulf of St. Lawrence cod: age specific distributions and environmental occurrences from 1971–1981. Can. Tech. Rep. Fish. Aquat. Sci. 1387: 43 p.

Trout, G. C. 1957. The Bear Island cod: migrations and movements. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Ser. II 21(6): 51 p.

Valerio, P. F., M. H. Kaò, and G. L. Fletcher. 1990. Thermal hysteresis activity in the skin of the cunner, *Tautogolabrus adspersus*. Can. J. Zool. 68: 1065–1067.

An Evaluation of the Stereocinematographic Method to Estimate Fish Swimming Speed

Daniel Boisclair

Université de Montréal, Département de sciences biologiques, C.P. 6128, Succursale «A», Montréal (Québec) H3C 3J7, Canada
and
Station de biologie des Laurentides de l'Université de Montréal, 440, avenue du Lac Croche, C.P. 159, St-Hippolyte (Québec) G0R 1P0, Canada

Boisclair, D. 1992. An evaluation of the stereocinematographic method to estimate fish swimming speed. Can. J. Fish. Aquat. Sci. 49: 523–531.

I evaluated the precision and accuracy of the stereocinematographic (SCG) method for estimating fish swimming speed. The SCG method implements the differences in images recorded by two cameras to determine the position of a target in an *x, y, z,* coordinate system. Movements and speeds were determined using variations in the position of the targets over time. Movements of rulers (95% CI = $\bar{X} \pm 4.6\%$) estimated in the laboratory did not differ significantly from measured values. The accuracy of the SCG method in the field was assessed by comparing simultaneous estimates of the speed of the head and of the tail of individual fish observed in in situ enclosures. Differences between these descriptors of fish swimming were always <2 body lengths (bl)$\cdot s^{-1}$ and, on average, did not differ significantly from 0. Swimming speeds (95% CI = $\bar{X} \pm 4.5\%$) ranged from 0.6 to 20.7 cm$\cdot s^{-1}$ (0.1–3.8 bl$\cdot s^{-1}$). Speed variations between two consecutive 1-s intervals ranged from −23.9 cm$\cdot s^{-1}$ (deceleration) to 23.6 cm$\cdot s^{-1}$ (acceleration). Positioning fish at 1- to 6-s intervals tended to decrease the variance of swimming speed estimates. A sample size of 100–150 speeds per hour was sufficient to accurately describe fish swimming in an in situ enclosure.

J'ai évalué la précision et l'exactitude de la méthode stéréocinématographique (SCG) pour estimer la vitesse de nage des poissons. La méthode SCG utilise les différences entre des images enregistrées par deux caméras pour situer une cible dans un espace *x, y, z*. Les mouvements et vitesses ont été déterminés par les variations de la position des cibles à différents moments. Des mouvements de règles (95% CI = $\bar{X} \pm 4,6$ %) estimés en laboratoire n'ont pas été significativement différents de valeurs mesurées. La précision de la méthode SCG sur le terrain a été vérifiée en comparant des estimés simultanés de la vitesse de la tête et de la queue de poissons observés dans des enclos *in situ*. La différence entre ces descripteurs de la nage des poissons n'a jamais été supérieur à 2 longueurs corporelles (lc)$\cdot s^{-1}$ et, en moyenne, n'a pas été significativement différente de 0. Les vitesses de nage (95% CI = $\bar{X} \pm 4,5$ %) ont varié entre 0,6 et 20,7 cm$\cdot s^{-1}$ (0,1 à 3,8 lc$\cdot s^{-1}$). Les variations de la vitesse entre deux intervalles consécutifs de 1 s ont varié entre −23,9 cm$\cdot s^{-1}$ (décélération) et 23,6 cm$\cdot s^{-1}$ (accélération). Le positionnement des poissons à intervalle de 1 à 6 s a diminué la variance des estimés de la vitesse de nage. Un échantillonnage de 100–150 estimés de vitesses par heure a été suffisant pour décrire de façon exacte la nage des poissons dans un enclos *in situ*.

Received May 24, 1991
Accepted October 4, 1991
(JB053)

Reçu le 24 mai 1991
Accepté le 4 octobre 1991

Activity costs have been hypothesized to have a significant influence on the energy available for fish growth (Kerr 1971; Boisclair and Leggett 1989, 1990, 1991) and reproduction (Ware 1982). Furthermore, optimal foraging models assume that the energetic cost of seeking and handling prey is a significant and variable component of fish energy budgets (Ware 1975, 1978; Werner and Hall 1974; Mittelbach 1981; Hoyle and Keast 1987; Persson and Greenberg 1990). However, few tests of the ecological implications of activity costs have been performed partly because of the practical difficulties of obtaining accurate estimates of fish swimming speed.

Swimming speed estimates are generally based on variations in fish position over time (McCleave and Horrall 1970; Young et al. 1972; Holliday et al. 1974; Diana et al. 1977; Diana 1980; Hawkins et al. 1980) or tail beat frequency (Feldmeth and Jenkins 1973; Hunter and Zweifel 1971; Hunter and Kimbrell 1980; Ross et al. 1981; Puckett and Dill 1985; Weatherley et al. 1982). Fish position estimates are inaccurate because they are made in two, instead of three, dimensions (but see Huse and Skiftesvik 1990). Furthermore, the use of either fish position or tail beat frequency in the field rarely allows one to differentiate rectilinear from erratic fish movements. Knowledge of the type of movement is essential in determining both true distance travelled per unit of time and energy expenditure because the cost of swimming at a given speed has been hypothesized to vary with the type of movements executed by fish (Smit 1965; Weatherley et al. 1982; Weatherley and Gill 1987; Webb 1991).

One solution to the problem of accurate description of fish movement is stereogrammetry. This approach is based on the principle that a single target viewed simultaneously by two cameras in parallel, separated by a known distance (i.e. binocular vision), does not appear at the same position in the image perceived by these cameras (Fig. 1). Measurements of target position in the two images can be used to determine the position of the target in an *x, y, z* coordinate system (Boyce 1964; Van Sciver 1972; Long and Aoyama 1985). The stereogrammetry approach has been used to estimate fish length (Klimley and Brown 1983; Ménard 1991) and to describe the three-dimensional structure of fish schools (Cullen et al. 1965; Graves 1977; Partridge et al. 1980; Dill et al. 1981; Aoki et al. 1986).

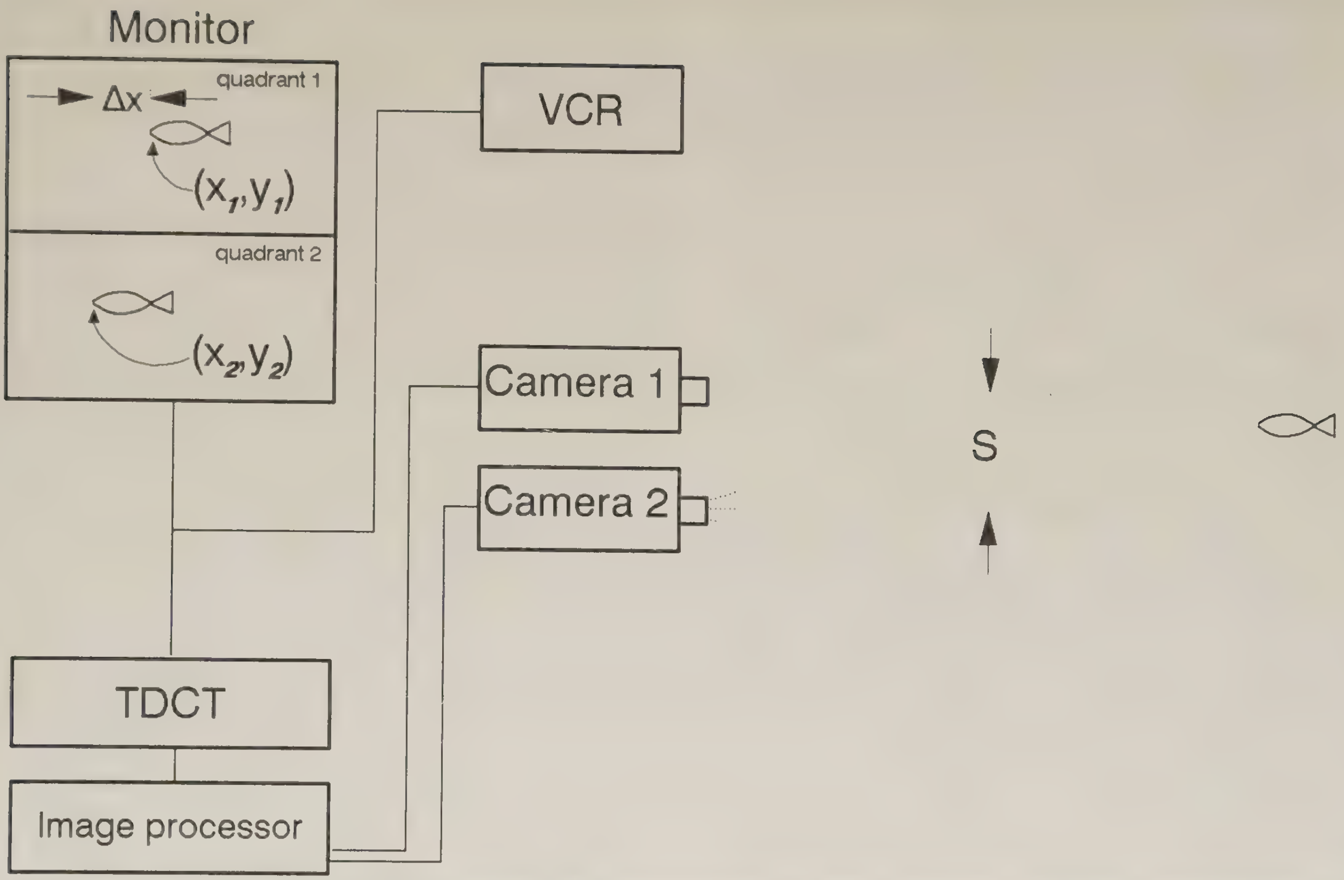


FIG. 1. Schematic representation of the SCG apparatus. The images perceived by the two cameras are combined by the videoprocessor (Quad), the camera titler (TDCT) copies the time on the images, and these images are recorded (S = optical axes separation; Δx = apparent target displacement).

The purpose of this paper is to (1) present the first attempt to estimate fish swimming speed using a stereogrammetric method, (2) evaluate the precision and accuracy of this method, (3) examine the influence of sample size and sampling frequency on swimming speed estimates, and (4) report swimming speeds and acceleration rates determined in in situ enclosures.

Methods

The stereogrammetric estimation of fish swimming speed differs from the determination of fish length and the description of the tridimensional structure of fish schools in that it requires numerous images taken at short time intervals. While stereogrammetric measurements are generally based on the analysis of stereopairs of photographs (i.e. stereophotography), in the present study, I utilized images taken using two videocameras (i.e. stereocinematography; SCG). Target position and its variation over time were used to estimate target movement (centimetres), swimming speeds (centimetres per second), and acceleration rates (centimetres per second squared).

Experimental Approach

The difference between movements derived using the SCG method and measured values was quantified in the laboratory. Testing of the SCG method to estimate fish swimming speed in the field was complicated by the absence of "measured" speeds with which estimated values could be compared. The accuracy of the SCG method was therefore assessed by testing the hypothesis that the average difference between simultaneous estimates of the speed of the head and of the tail of individual fish is not significantly different from 0. However, during 180° turns executed within 1 s, while the position of the head *or* of the tail remains relatively constant, the speed of the head and of the tail of a fish can, theoretically, differ by as much as 2 body lengths $(\text{bl})\cdot\text{s}^{-1}$. Consequently, the accuracy of the SCG method was also measured by testing the hypothesis that the difference between simultaneous estimates of the speed of the head and of the tail of a fish is not greater than $2\ \text{bl}\cdot\text{s}^{-1}$.

Experimental Procedure

Laboratory experiment

The laboratory experiment consisted of filming three rulers measuring 5, 10, and 15 cm at distances of 50, 100, 150, and 200 cm from the cameras. For each ruler length/distance combination, the ruler was moved 1, 5, 10, and 20 cm perpendicularly to the optical axes of the cameras (Fig. 1). These movements of the rulers are hereafter referred to as measured movements.

Field experiment

The field experiment was conducted in a 1.5-m^3 nylon enclosure (1 × 1 × 1.5 m; 0.06-cm^2 mesh) anchored horizontally on the 4-m depth isobath of a mesotrophic lake located at La Station de biologie des Laurentides de l'Université de Montréal (70 km northwest of Montreal) in the Lower Laurentians region of Quebec.

On August 15, 1990, SCUBA divers introduced five young-of-the-year (YOY) (1.44 g wet weight, SD = 0.33; 55.8 mm total length, SD = 4.96) brook trout (*Salvelinus fontinalis*) into the enclosure through an opening at one extremity of the cage. The cameras were mounted inside the enclosure following the introduction of the fish. The fish were filmed continuously on the next day (August 16, 1990) from 07:00 to 09:00. This delay was assumed to be sufficient to allow the fish to recuperate from the stress related to their transfer to the enclosure and the sediments lifted by the divers to settle.

Calibration

Stereocinematographic positioning of a target requires the estimation of the distance that separates the optical axes of the two cameras (herafter referred to as optical axes separation). Optical axes separation (S) (Fig. 1) varies with experimental conditions. For instance, the optical axes of two cameras are rarely, if ever, perfectly parallel. Optical axes separation can either increase (divergent optical axes) or decrease (convergent optical axes) with the distance between the cameras and the targets. Furthermore, the relationship between S and the distance between the target and the camera can be expected to change with the refraction index of the medium in which the measurements are performed (Van Sciver 1972; Klimley and Brown 1983).

In my work, the observations made under laboratory conditions were performed in the air; while in the field, they were made in the water. Consequently, the relationships between optical axes separation and target distance from the cameras were estimated independently for each experimental condition. Calibration was executed by filming different rulers at a series of measured distances from the cameras (Klimley and Brown 1983; Ménard 1991). Under laboratory conditions, three rulers measuring 5, 10, and 15 cm were filmed at distances from the cameras ranging from 25 to 300 cm at 25-cm intervals. Under field conditions, two rulers measuring 5 and 12.4 cm were filmed at distances of 25, 50, 75, 100, and 150 cm from the cameras.

Apparatus

The two perspectives on a given target required to perform its stereocinematographic positioning in an x, y, z coordinate system were provided by two Panasonic WV-BL602 cameras arranged in parallel 10 cm apart (center to center; Fig. 1). The cameras were mounted with Cosmicar automatic iris EX-2 lenses (6 mm, F 1.2; angle of vision: 56° horizontally, 46.3° vertically). A videoprocessor Panasonic Quad WJ-450 (hereafter referred to as the Quad) ensured temporal synchrony between the two cameras. The Quad combines images received simultaneously from different sources (here two cameras) and presents these images in two different quadrants of a single image on a monitor (Fig. 1). A time and day camera titler (TDCT), installed in series with the system, indicated the date and the time (hour:minute:second) on each image processed by the Quad. This final image was recorded using a Sony CCD-F70 8-mm Handycam (VCR; Fig. 1). During underwater in situ experiments, the cameras were placed in a waterproof Plexiglas casing with a glass side through which pictures were recorded.

Image Analysis

Image measurements necessary to calibrate the system and determine the position, movement, and speed of a target from pairs of images were performed using the Jandel Video Analysis Software (Java). The position of a target in the images recorded was defined by two pairs of coordinates, one for each quadrant displayed on the monitor used to perform the image analyses (Fig. 1). Each pair of coordinates was determined relative to an origin located in the middle of the quadrant from which it was taken. The unit of the coordinates, hereafter referred to as ''centimetres$_i$ (cm$_i$),'' identifies the lengths obtained directly on the monitor. In contrast, ''centimetres (cm)'' is used as a unit representing real lengths (i.e. at the scale of the laboratory, or of the enclosure).

The x, y, z position of each ruler was described by both the position of the beginning and of the end of that ruler. Similarly, the x, y, z position of a fish was described by the position of the head and of the tail of that fish. The x, y, z position of a fish (head or tail) was determined at 1-s intervals. When more than one fish was visible during a given time period, each fish was digitized sequentially until the successive x, y, z positions of all fish observed during that time period were estimated.

Computations

Estimation of movement, speed, and acceleration

Target movement (M_t', centimetres) between two successive time intervals t and $t + 1$ was estimated as

$$(1) \quad M_t' = (S_t \cdot m_t')/\Delta\bar{x}_t$$

where $\Delta\bar{x}_t$ (cm$_i$) is the average apparent displacement of the target at time t and $t+1$, S_t (cm) is the optical axes separation, and m_t' (cm$_i$) is the movement of the target between t and $t+1$ in image units.

$\Delta\bar{x}_t$ was estimated as

$$(2) \quad \Delta\bar{x}_t = (\Delta x_t + \Delta x_{t+1})/2$$

where Δx_t and Δx_{t+1} (cm$_i$) are the absolute differences between the x-coordinates of the target on both quadrants ($|x_1 - x_2|$; Fig. 1) at time t and $t + 1$, respectively.

S_t was estimated using empirical relationships derived from the calibration procedure. During the calibration, S was estimated for each ruler length/distance from cameras combination as

$$(3) \quad S = (L/l) \cdot \Delta x$$

where L (cm) is the length of a ruler used to calibrate the video system and l (cm$_i$) is the length of this ruler as it appeared on the monitor (Van Sciver 1972; Klimley and Brown 1983; Ménard 1991).

The equations used to estimate S under laboratory and field conditions were, respectively, $S = 7.14 \cdot (\Delta x)^{-2} + 10.22$ ($F_{1,33} = 495.26$; $p < 0.0001$: $r^2 = 0.94$) and $S = -0.065 \cdot (\Delta x)^2 + 1.02 \cdot \Delta x + 5.39$ ($F_{1,5} = 134.07$, $p < 0.0001$, $r^2 = 0.98$).

m_t' was estimated as

$$(4) \quad m_t' = \sqrt{[(\bar{x}_{t+1} - \bar{x}_t)^2 + (\bar{y}_{t+1} - \bar{y}_t)^2 + (\bar{z}_{t+1} - \bar{z}_t)^2]}$$

where $\bar{x}$, $\bar{y}$, and $\bar{z}$ (cm$_i$) are the average values of the target coordinates relative to the center of the two quadrants displayed on the monitor used to perform the analysis of images recorded at time t and $t + 1$ (Fig. 1). The $\bar{x}$, $\bar{y}$, $\bar{z}$ coordinates were determined using a modified version of the algorithm developed by Boyce (1964), Van Sciver (1972), and Long and Aoyama (1985) to estimate fish length and three-dimensional structure of fish schools (Appendix).

Speeds and acceleration rates were estimated at 1-s time intervals for each fish observed. The speed of the head (VH_t', centimetres per second) or tail (VT_t', centimetres per second) of a fish was estimated by dividing head or tail movement by the time interval Δt between successive positioning of the head or tail of that fish. Swimming speed (V_t', centimetres per second) was defined as the average speed of the head and of the tail of a fish. Acceleration rates (A_t', centimetres per second squared) were estimated by dividing the change in swimming speed between two successive time intervals by the length of that time interval.

Influence of Sample Size and Sampling Frequency

The influence of sample size on swimming speed and acceleration estimates was examined by comparing the mean and standard deviation of these attributes among a series of pseudo-samples of variable sizes. The size of the eight speed pseudo-samples compared ranged from 25 to 300, while that of the seven acceleration pseudo-samples ranged from 25 to 250. The potential influence of activity variations during the recording session (07:00–09:00) was minimized by selecting the movements required to execute this analysis within the 08:00–09:00 time interval.

The influence of sampling frequencies on swimming speed and acceleration estimates was assessed using five series of fish observations that lasted 13 s. For each series, swimming speeds and acceleration rates were calculated using head and tail positions determined at 1-, 2-, 3-, and 6-s intervals.

Error Analysis

Error associated with swimming speed and acceleration estimates derived using the SCG method was evaluated by bootstrapping (Efron 1981). I estimated the *x, y, z* coordinates of a single fish (head and tail) 20 times during an 11-s recording sequence. I then executed a bootstrap simulation for each of the ten 1-s time intervals. A bootstrap simulation proceeded by estimating swimming speed during a 1-s time interval using randomly selected positions of the head and of the tail of the fish at time t and $t + 1$ from within the 20 possibilities derived experimentally for each t. This procedure, repeated 1000 times for each time interval, produced 1000 swimming speed and acceleration estimates for each time interval (herafter referred to as the bootstrap samples).

Data Analysis

I used linear regression analysis to compare estimates of target movement derived using the SCG method under laboratory conditions with measured values. Paired *t*-tests were used to evaluate the hypothesis that the average difference between simultaneous speed estimates of the head and of the tail of individual fish was 0. Swimming speed and acceleration estimates derived using different sample sizes and sampling frequencies were compared using parametric and non parametric (Kruskal–Wallis) one-way analysis of variance (ANOVA). Normality was verified using Kolmogorov–Smirnov tests and homogeneity of variance was tested using $F_{\max}$ tests. The 10 bootstrap samples of swimming speeds and the nine bootstrap samples of acceleration rates were described using their arithmetic mean and 95% confidence intervals (CI). The 95% CI of a bootstrap sample was defined as the 2.5 and 97.5 percentile of its frequency distribution ($n = 1000$). Swimming speeds or acceleration rates of two time intervals were declared different when their 95% CI did not overlap.

Results

Laboratory Experiment

There was a strong positive relationship between movements estimated under laboratory conditions and measured values (Fig. 2). The intercept of this relationship did not differ significantly from (SE = 0.14, df = 118, $t_s = 1.91, p > 0.05$). While the slope of the relationship between estimated and measured movements was significantly different from 1 (SE = 0.01, df = 118, $t_s = 2.3, p < 0.05$), its confidence intervals (95% CI = 0.96–0.99) indicated that, for practical purposes, the slope could be considered equal to 1. The 95% CI of the movements estimated using the SGC method always included the measured values.

Field Experiment

Two hours of recording allowed the calculation of 383 head and tail speed estimates distributed among 57 position time series. The length of the position time series ranged from 2 to 38 s. Most (82%) of these time series covered less than 10 s and few (7%) were longer than 20 s.

Comparison of head and tail speeds

Simultaneous speed estimates of the head and of the tail of individual fish were generally tightly coupled and ranged from 0.3 to 24.37 and from 0.6 to 20.44 $\mathrm{cm \cdot s^{-1}}$, respectively (Fig. 3). The average difference between these two descriptors of fish swimming speed (absolute value = 0.025 $\mathrm{cm \cdot s^{-1}}$) did not significantly differ from 0 (SD = 2.24, df = 382, $t_s = 0.01, p > 0.9$).

Differences between head and tail speed estimates were smaller than 1 $\mathrm{cm \cdot s^{-1}}$ for 52% of the speed pairs. Speed pairs that differed by less than 5 and 10 $\mathrm{cm \cdot s^{-1}}$ comprised, respectively, 97 and 99.7% of the speed values. On a relative basis, differences between head and tail speed estimates were smaller than 50% for 83% of the speed pairs.

Fish swimming speed and acceleration

Fish swimming speeds ranged from 0.6 to 20.7 $\mathrm{cm \cdot s^{-1}}$ and averaged 6.1 $\mathrm{cm \cdot s^{-1}}$. Most speed estimates occurred within 0–5 (44.8%) and 5–10 (43.3%) $\mathrm{cm \cdot s^{-1}}$. Less than 3% of the speeds recorded were faster than 15 $\mathrm{cm \cdot s^{-1}}$. Acceleration rates ranged from −23.9 (deceleration) to 23.6 $\mathrm{cm \cdot s^{-2}}$. However, 80.4% of acceleration rates occurred within the −5 to 5 $\mathrm{cm \cdot s^{-2}}$ range.

Influence of sample size and sampling frequency on swimming speed and acceleration estimates

Mean swimming speeds derived using 25–300 speed estimates ranged from 5.17 to 5.72 $\mathrm{cm \cdot s^{-1}}$ (Table 1). Corresponding values for acceleration rates were −0.37 to 0.19 $\mathrm{cm \cdot s^{-2}}$ (Table 1). While sample size did not have a significant influence on mean speed ($F_{7,1142} = 0.36, p > 0.90$) or acceleration ($F_{6,843} = 0.08, p > 0.99$) estimates, the standard deviation of these descriptors of fish swimming tended to stabilize when sample size reached 100–150 estimates (Table 1).

The different sampling frequencies resulted in 7.6% (series 1) to 74.1% (series 2) variations in average fish swimming speed (Table 2). Furthermore, the variance of the swimming speeds estimated following different sampling schedules often decreased with increasing sampling intervals. Parametric one-way ANOVA performed on series 1, 2, and 4 (homogeneous variance, $2.6 < F_{\max} < 16.6$, $p > 0.05$) revealed no significant difference among the swimming speeds derived using the three sampling frequencies tested ($0.03 < F_{3,20} < 0.42$, $0.74 < p < 0.99$). Nonparametric one-way ANOVA (Kruskal–Wallis test) executed on series 3 and 5 (heterogeneous variance, $1936 < F_{\max} < 2147$, $p < 0.01$) indicated no significant difference among the swimming speeds estimated using different sampling frequencies ($0.35 < \chi^2 < 0.41$, $0.94 < p < 0.95$).

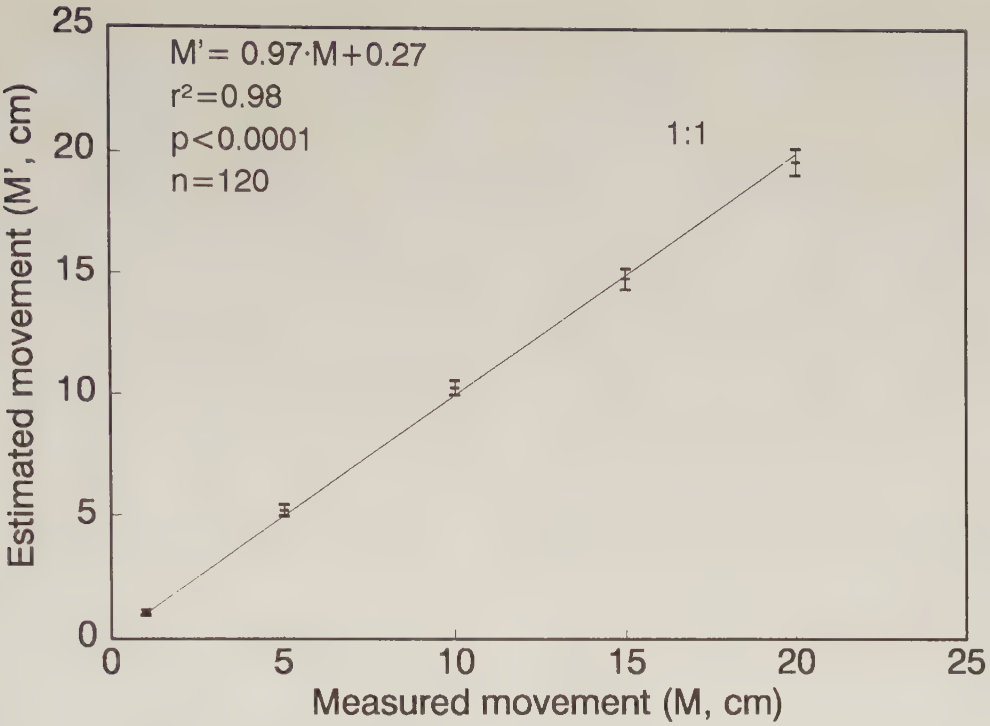


FIG. 2. Relationship between estimated and measured target movements under laboratory conditions. Vertical bars represent 95% CI of estimated values.

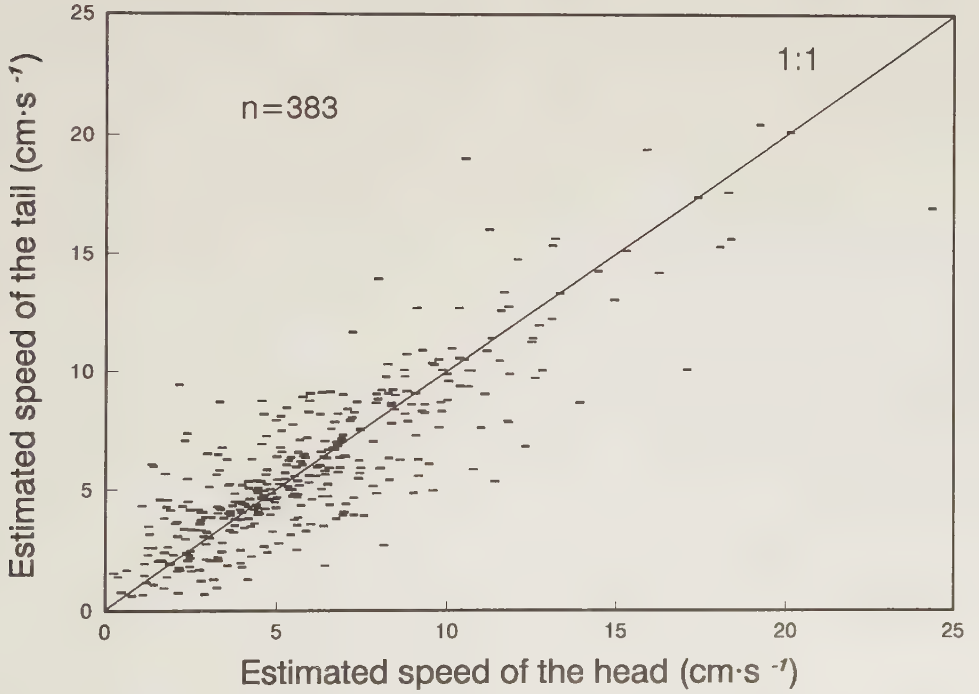


FIG. 3. Relationship between simultaneous speed estimates of the head and of the tail of individual fish.

Acceleration estimates obtained while fish position was determined at 1-s intervals ranged from −0.1 (series 4) to 0.7 (series 2). Less frequent sampling caused a 1.5- (series 2) to 25-fold (series 3) variation in mean acceleration rates (Table 3). I found no significant difference among the acceleration estimates derived using different sampling frequencies (series 1, 2, 4, 5: homogeneous variance, $2.6 < F_{max} < 18.5$, $p > 0.05$; parametric one-way ANOVA, $0.04 < F_{3,20} < 0.39$, $0.76 < p < 0.99$; series: heterogeneous variance, $F_{max} = 595.4$, $p < 0.01$; nonparametric one-way ANOVA, $\chi^2 = 0.11$, $p > 0.99$).

The observed lack of significant influence of the sampling frequency on swimming speed and acceleration estimates can be largely imputed to the high variances associated with these estimates.

TABLE 1. Mean swimming speed (V', backtransformed from natural logarithm) and acceleration (A') estimates derived using a sample size ranging from 25 to 300. Fish movements used in this analysis were recorded between 08:00 and 09:00 (ln SD = standard deviation on a logarithmic basis).

Sample size (n)	V' ($\mathrm{cm \cdot s^{-1}}$)	ln SD	A' ($\mathrm{cm \cdot s^{-2}}$)	SD
25	5.72	0.61	−0.37	4.24
50	5.17	0.72	0.19	5.44
75	5.25	0.69	0.07	4.93
100	5.30	0.65	0.01	4.59
150	5.48	0.65	−0.19	5.89
200	5.70	0.63	−0.22	5.76
250	5.58	0.64	−0.14	5.58
300	5.32	0.64		

TABLE 2. Mean swimming speed ($\mathrm{cm \cdot s^{-1}}$) estimated when fish position (head and tail) was determined at 1-, 2-, 3-, or 6-s intervals. Data are from five series of fish observations of 13-s duration. Standard deviation and number of swimming speed estimates are presented in parentheses and brackets, respectively.

	Sampling frequency(s)				
Series	1 [n = 12]	2 [n = 6]	3 [n = 4]	6 [n = 2]	Maximum variation (%)[a]
1	6.5	6.8	6.8	6.3	7.6
	(2.3)	(2.3)	(3.7)	(3.5)	
2	8.4	8.7	6.2	4.5	63.6
	(7.9)	(10.6)	(2.6)	(3.0)	
3	9.1	11.1	5.1	5.5	74.1
	(10.0)	(13.9)	(0.5)	(0.3)	
4	7.8	9.5	7.1	8.2	28.9
	(3.6)	(4.6)	(1.9)	(2.3)	
5	5.1	4.2	5.4	3.8	34.8
	(2.7)	(1.4)	(4.4)	(0.1)	

[a]Calculated as 200·[(max. est. − min. est.)/(max. est. + min. est.)].

Error analysis

Mean swimming speeds derived using the bootstrap simulations ranged from 3.93 ($t = 6$) to 8.53 $\mathrm{cm \cdot s^{-1}}$ ($t = 10$). The 95% CI of the swimming speed data averaged ±4.5% of the mean (Table 4). Corresponding acceleration values ranged from −1.54 ($t = 7$) to 3.75 $\mathrm{cm \cdot s^{-2}}$ ($t = 8$). The average 95% CI of acceleration estimates varied significantly among the 10 time intervals examined. Multiple paired tests based on the bootstrap samples indicated that mean speeds that differed by more than 0.6 $\mathrm{cm \cdot s^{-1}}$ (approximately 7% of the largest value compared) could be considered significantly different. The corresponding critical difference for acceleration rates was 0.7 $\mathrm{cm \cdot s^{-2}}$ (approximately 40% of the largest value compared).

Discussion

My analyses indicate that the SCG method provides precise and accurate estimates of target movement under laboratory conditions and of fish swimming speeds and acceleration rates under field situations. These conclusions arise, not only from the isometric relationship (slope = 1, intercept = 0) between measured and estimated movements derived under laboratory conditions, but also from the similarity between simultaneous speed estimates of the head and tail of individual fish under field situations.

TABLE 3. Mean fish acceleration rates ($\mathrm{cm \cdot s^{-2}}$) estimated when fish position (head and tail) was determined at 1-, 2-, 3-, or 6-s intervals. Data are from five series of fish observations of 13-s duration. Standard deviation and number of swimming speed estimates are presented in parentheses and brackets, respectively.

	Sampling frequency(s)				
Series	1 [n = 11]	2 [n = 5]	3 [n = 3]	6 [n = 1]	Maximum variation (%)[a]
1	0.2	0.5	−0.1	5.0	208
	(4.0)	(4.5)	(6.4)		
2	0.7	0.6	1.6	4.2	150
	(9.1)	(17.2)	(4.0)		
3	0.1	0.8	−0.2	0.4	333
	(13.9)	(24.4)	(1.0)		
4	−0.1	2.2	−0.2	3.3	226
	(5.8)	(3.1)	(3.9)		
5	0.3	−0.2	2.7	−0.2	232
	(4.1)	(2.7)	(5.1)		

[a]Calculated as 200·[(max. est. − min. est.)/(max. est. + min. est.)].

Observed differences in the order of 5–10 $\mathrm{cm \cdot s^{-1}}$ between simultaneous head and tail speed estimates of individual fish are expected and do not represent systematic errors. During 180° turns, the speed of the head and of the tail of 5.5-cm fish (average length of the fish used in my experiments) can, theoretically, differ by as much as 11 $\mathrm{cm \cdot s^{-1}}$ (i.e. 2 $\mathrm{bl \cdot s^{-1}}$). Consequently, the observed differences between the speed of the head and of the tail of a fish may, in fact, represent its ability to execute rapid (within a 1-s interval) 0–180° turns while the position of the head *or* the tail remains relatively constant. The capability of fish to execute such movements is supported by the work of Fuiman and Webb (1988). Their description of the swimming characteristics of larval, juvenile, and adult zebra danios (*Danio rerio*) under laboratory conditions indicated that turning angles ranging from 100 to 180° accounted for approximately 20–25% of the turns. My work not only emphasizes that turns in the 100–180° range are common, but further indicates that these changes in the orientation of fish are possible even at high swimming speeds (15–25 $\mathrm{cm \cdot s^{-1}}$).

In the present study, the position of all fish observed was estimated at 1-s intervals. While my work indicates that the sampling frequency of 1 s should be utilized to insure that the estimates accurately represent the true variance of swimming speeds and acceleration rates, my analyses also emphasize that a sample size of 100–150 swimming speed or acceleration estimates per hour is sufficient to adequately describe these descriptors of fish swimming.

Comparison with Other Methods

The SCG method differs from other procedures in three important ways. First, even when direct visual observations are possible (Persson 1987; Bergman 1987; Persson and Greenberg 1990), the SCG method allows a more detailed qualitative as well as quantitative description of fish movement. Second, the SCG method is the only procedure that permits the estimation of fish movements in three dimensions (see Weatherley and Gill 1987 for a review). One exception is the method utilized by Huse and Skiftesvik (1990) to estimate the movements of fish larvae. Their method requires that an operator follow an individual fish held in an aquarium using a mobile camera mounted on a frame. The camera frame, mount, and focusing ring are coupled with independent potentiometers. These potentiome-

TABLE 4. Mean swimming speed (V') and acceleration estimates (A') derived at 1-s intervals during an 11-s recording sequence using bootstrap simulations (SD = standard deviation of the bootstrap samples: n = 1000).

Time (s)	V' ($cm \cdot s^{-1}$)	SD	95% CI	A' ($cm \cdot s^{-2}$)	SD	95% CI
1	8.13	0.14	7.84 to 8.41	−1.52	0.18	−1.89 to −1.17
2	6.61	0.10	6.41 to 6.81	−0.92	0.13	−1.18 to −0.64
3	5.69	0.08	5.55 to 5.88	−1.76	0.13	−2.02 to −1.51
4	3.93	0.11	3.73 to 4.16	3.52	0.17	3.17 to 3.82
5	7.45	0.13	7.16 to 7.69	−4.07	0.19	−4.43 to −3.68
6	3.38	0.14	3.11 to 3.65	2.39	0.19	2.03 to 2.80
7	5.77	0.13	5.53 to 6.05	−1.54	0.21	−1.97 to −1.14
8	4.23	0.16	3.89 to 4.53	3.75	0.23	3.28 to 4.20
9	7.98	0.17	7.62 to 8.32	0.55	0.20	0.17 to 0.93
10	8.53	0.11	8.36 to 8.76			

ters transform the movement of the camera, frame, and mount into x and y coordinates, while the focusing ring provides the z coordinate. The method presented by Huse and Skiftesvik (1990), however, might be difficult to apply to larger, faster fish and to field situations. Third, in contrast with the telemetric and electromyogram procedure, the SCG method does not require the implantation or attachment to the fish of any transmitting or recording device. Consequently, the SCG method can be used with a wide range of fish sizes without influencing their behavior, especially when used in the field with no enclosures. Furthermore, because the SCG method is based on direct observations, it is possible to identify the type of movements executed by fish and therefore to apply adequate correction factors when transforming fish swimming speeds to swimming costs. This point is important, since, as suggested by Webb (1991), the swimming costs determined using the product of speed and swimming costs derived from flume experiments (see Beamish 1978 for a review) should be multiplied by a factor of 3 to account for the difference between the costs of routine movements (changes in speed and direction) and steady movements (constant speed and rectilinear trajectory).

The most serious limitation of the SCG method is its dependence on visibility. The problem of low light intensity can be either diminished by using cameras with photomultipliers or solved, at least under laboratory conditions, by using infrared illuminators and infrared-sensitive cameras (Huse and Skiftesvik 1990; Collins et al. 1991). The problem of poor water transparency under field conditions is presently impossible to resolve. Water transparency is critical, since it determines the volume of water "sampled" by the videocamera system. While precise calculations of the volume "sampled" by the videocamera system are impeded by distortion phenomena on the margin of the field covered by the cameras, and by the difference between the vertical and horizontal opening of the lenses (see Apparatus in the Methods section), it can, at least, be approximated.

The experiments presented in this paper were performed while the Secchi depth in the littoral zone of the study lake was 3.1 m. Under this condition, it was possible to discriminate a 5.0- to 6.0-cm fish at distances up to 2.5 m from the cameras. Assuming an average lens opening of 51.2°, minimum height and radius of the cone sampled can be estimated, respectively, as 2.25 m ($2.5 \cdot \cos 25.6°$) and 1.0 m ($\text{height} \cdot \sin 25.6°$). Corresponding maximum values are 2.5 m and 1.1 m. Consequently, the volume (volume of a cone = $\frac{1}{3} \cdot \pi \cdot \text{radius}^2 \cdot \text{height}$) "sampled" by the videocamera system, excluding the limits of the enclosure, is expected to be contained in a 2.4–3.2 m^3 range. Considering the relatively small volume of water "sampled" by the videocamera system, the SCG method is expected to be useful for estimating fish swimming speed only in situations where fish abundance is high, such as in littoral zones of lakes, or, as in my study, when fish abundance is controlled experimentally. Clearly, the method presented in this paper is not intended to replace, but to complement already existing procedures.

Acknowledgments

I thank Alex Châtelier, Martha Krohn, Ming Tang, and Catherine Tessier for their valuable assistance in the laboratory and the field. I also thank Chantal Ménard and John Downing for generously sharing their expertise on underwater videocamera systems and image analysis and Robert Brunet for verifying the validity of the geometrical equations utilized in this work. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Quebec Ministry of Education (FCAR) through grants to the Freshwater Ecology Group of the University of Montreal, and the University of Montreal through CAFIR, Research Development Funds, and NSERC (Internal Funds).

References

AOKI, I., T. INAGAKI, AND L. V. LONG. 1986. Measurements of three-dimensional structure of free-swimming pelagic fish schools in a natural environment. Bull. Jpn. Soc. Sci. Fish. 52: 2069–2077.

BEAMISH, F. W. H. 1978. Swimming capacity, p. 101–187. *In* W. S. Hoar and D. J. Randall [ed.] Fish Physiology. Vol. VII. Academic Press, New York, NY.

BERGMAN, E. 1987. Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*. Environ. Biol. Fishes 19: 45–53.

BOISCLAIR, D., AND W. C. LEGGETT. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Can. J. Fish. Aquat. Sci. 46: 1859–1867.

1990. On the relationship between growth and consumption rates: response to comments by R. S. Hayward (1989). Can. J. Fish. Aquat. Sci. 47: 230–233.

1991. If computers could swim or fish could be programmed: a response to comments by Hewett et al. (1991). Can. J. Fish. Aquat. Sci. 48: 1337–1344.

BOYCE, R. E. 1964. Simple scale determination on underwater stereo pairs. Deep-Sea Res. 11: 89–91.

COLLINS, N C., S. G. HINCH, AND K. A. BAIA. 1991. Non-instrusive time-lapse video monitoring of shallow aquatic environments. Can. Tech. Rep. Fish. Aquat. Sci. 1821

CULLEN, J. M., E. SHAW, AND H. A. BALDWIN. 1965. Methods for measuring the three-dimensional structure of fish schools. Anim. Behav. 13: 534–543.

DIANA, J. S. 1980. Diel activity and swimming speeds of northern pike (*Esox lucius*) in Lac Ste-Anne, Alberta. Can. J. Fish. Aquat. Sci. 37: 1454–1458.

DIANA, J. S., W. C. MACKAY, AND M. EHRMAN. 1977. Movements and habitat preference of northern pike (*Esox lucius* L.) in Lac Ste-Anne, Alberta. Trans. Am. Fish. Soc. 106: 560–565.

DILL, L. M., R. L. DUNBRACK, AND P. F. MAJOR. 1981. A new stereophotographic technique for analyzing the three-dimensional structure of fish schools. Environ. Biol. Fishes 6: 7–13.

EFRON, B. 1981. Nonparametric estimates of standard error: the jacknife, the bootstrap and other methods. Biometrika 68: 589–599.

FELDMETH, C. R., AND T. M. JENKINS. 1973. An estimate of energy expenditure by rainbow trout (*Salmo gairdneri*) in a small mountain stream. J. Fish. Res. Board Can. 30: 1755–1759.

FUIMAN, L. A., AND P. W. WEBB. 1988. Ontogeny of routine swimming activity performance in zebra danios (Teleostei: Cyprinidae). Anim. Behav. 36: 250–261.

GRAVES, J. 1977. Photographic method for measuring spacing and density within pelagic fish schools at sea. U.S. Fish. Bull. 75: 230–234.

HAWKINS, A. D., G. G. URQUHART, AND G. W. SMITH. 1980. Ultrasonic tracking of juvenile cod by means of a large spaced hydrophone array, p. 461–470. *In* C. J. Amlaner Jr. and D. W. MacDonald [ed.] A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford.

HOLLIDAY, F. G. T., P. TYTLER, AND A. H. YOUNG. 1974. Activity levels in trout (*Salmo trutta*) in Airthrey Loch, Stirling and Loch Leven, Kinross. Proc. R. Soc. Edinb. (B) 74: 315–331.

HOYLE, J. A., AND A. KEAST. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). Can. J. Zool. 65: 1972–1977.

HUNTER, J. R., AND C. A. KIMBRELL. 1980. Early life history of pacific mackerel, *Scomber japonicus*. Fish. Bull. 78: 89–101.

HUNTER, J. R., AND J. R. ZWEIFEL. 1971. Swimming speed, tail beat amplitude and size in jack mackerel, *Trachurus symetricus*, and other fishes. Fish Wild. Serv. U.S. Fish. Bull. 69: 253–266.

HUSE, I., AND A. B. SKIFTESVIK. 1990. A PC-aided video based system for behaviour observation of fish larvae and small aquatic invertebrates. Aquacult. Eng. 9: 131–142.

KERR, S. R. 1971. A simulation model of lake trout growth. J. Fish. Res. Board Can. 28: 815–819.

KLIMLEY, A. P., AND S. T. BROWN. 1983. Stereophotography for the field biologist: measurement of lengths and three-dimensional positions of free-swimming sharks. Mar. Biol. 74: 175–185.

LONG, L. V., AND T. AOYAMA. 1985. Photographic measurement for obtaining the length, aspect and bearing of free-swimming fish from their spatial position. Bull. Jpn. Soc. Sci. Fish. 51: 191–195.

MCCLEAVE, J. D., AND R. M. HORRALL. 1970. Ultrasonic tracking of homing cut throat trout (*Salmo clarki*) in Yellowstone Lake. J. Fish. Res. Board Can. 27: 715–730.

MÉNARD, C. 1991. Utilisation de la vidéo pour mesurer les poissons *in situ*. M.Sc. thesis, Université de Montréal, Montréal (Qué.). 88 p.

MITTELBACH, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370–1386.

PARTRIDGE, B. L., T. PITCHER, J. M. CULLEN, AND J. WILSON. 1980. The three-dimensional structure of fish schools. Behav. Ecol. Sociobiol. 6: 277–288.

PERSSON, L. 1987. The effects of resource availability and distribution of size class interactions in perch (*Perca fluviatilis*). Oikos 48: 148–160.

PERSSON, L., AND L. A. GREENBERG. 1990. Optimal foraging and habitat shift in perch (*Perca fluviatilis*) in a resource gradient. Ecology 71: 1699–1713.

PUCKETT, K. J., AND L. M. DILL. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behavior 92: 97–111.

ROSS, L. G., W. WATTS, AND A. H. YOUNG. 1981. An ultrasonic biotelemetry system for the continuous monitoring of tail-beat rate from free-swimming fish. J. Fish Biol. 18: 479–490.

SMIT, H. 1965. Some experiments on the oxygen consumption of goldfish (*Carassius auratus* L.) in relation to swimming speed. Can. J. Zool. 43: 623–633.

VAN SCIVER, W. J. 1972. Scale determination of unrecognized undersea objects by stereographic photography. Mar. Technol. Soc. J. 6: 14–16.

WARE, D. M. 1975. Growth, metabolism and optimal swimming speed of a pelagic fish. J. Fish. Res. Board Can. 32: 33–41.

1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. J. Fish. Res. Board Can. 35: 220–228.

1982. Power and evolutionary fitness of teleosts. Can. J. Fish. Aquat. Sci. 39: 3–13.

WEATHERLEY, A. H., AND H. S. GILL. 1987. The biology of fish growth. Academic Press, New York, NY. 443 p.

WEATHERLEY, A. H., S. C. ROGERS, D. G. PINCOCK, AND J. R. PATCH. 1982. Oxygen consumption of active rainbow trout, *Salmo gairdneri* Richardson, derived from electromyograms obtained by radiotelemetry. J. Fish Biol. 20: 479–489.

WEBB, P. W. 1991. Composition and mechanics of routine swimming of rainbow trout, *Oncorhynchus mykiss*. Can. J. Fish. Aquat. Sci. 48: 583–590.

WERNER, E. E., AND D. J. HALL. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042–1052.

YOUNG, A. H., P. TYTLER, F. G. T. HOLLIDAY, AND A. MACFARLANE. 1972. A small sonic tag for measurement of locomotor behaviour in fish. J. Fish Biol. 4: 57–65.

Appendix

This appendix describes the computations executed to estimate the swimming speed of a fish taking, for illustrative purposes, the position of the head of that fish as a reference. The computations are based on the average x, y, z position of a target relative to two coordinate systems which have, as an origin (0, 0, 0), the middle of each quadrant displayed on a monitor receiving simultaneous images from two cameras mounted in parallel (Fig. 1). The computations involve two units: "cm_i" identifies lengths obtained directly on the monitor used to perform the image analyses, while "cm" is used as a unit representing real lengths.

The following coordinates were taken for the head of a fish observed during 3 s:

Time t (s)	x_1 (cm_i)	y_1 (cm_i)	x_2 (cm_i)	y_2 (cm_i)
1	−0.30	2.14	−3.31	2.11
2	0.53	2.61	−2.41	2.72
3	−2.29	4.01	−5.36	3.92

The two pairs of coordinates (x_1, y_1) and (x_2, y_2) are, respectively, the position of the head of the fish on the first and second images recorded (Fig. 1). Each coordinate has as an origin the center of the quadrant from which it was taken. Average x- ($\bar{x}$, cm_i) and y- ($\bar{y}$, cm_i) coordinates were calculated, respectively, as

$$\bar{x} = (x_1 + x_2)/2$$

and

$$\bar{y} = (y_1 + y_2)/2.$$

Apparent target displacement (Δx, cm_i) (Fig. 1.) was calculated as

$$\Delta x = |x_1 - x_2|.$$

Average length of the diagonals between the origins and the target ($\bar{d}$, cm_i) was calculated as

$$\bar{d} = (d_1 + d_2)/2$$

where the diagonals on the first (d_1, cm_i) and second images (d_2, cm_i) were calculated, respectively, as

$$d_1 = \sqrt{x_1^2 + y_1^2}$$

and

$$d_2 = \sqrt{x_2^2 + y_2^2}.$$

The measurements obtained from the images recorded were further used to estimate the length of the sides of two triangles. The first triangle is in a plane which is at an angle with that of the images on the monitor. The hypotenuse and one of the sides of this triangle correspond, respectively, to $\bar{d}$ and $\bar{y}$. The length of the third side ($\bar{d}^*$, cm$_i$) of this triangle was estimated as

$$\bar{d}^* = \sqrt{\bar{d}^2 - \bar{y}^2}.$$

The second triangle is in a plane perpendicular to that of the images on the monitor. The hypotenuse and one of the sides of this second triangle correspond, respectively, to $\bar{d}^*$ and $\bar{x}$. The length of the third side ($\bar{z}$, cm$_i$) of this triangle was estimated as

$$\bar{z} = \sqrt{\bar{d}^{*2} - \bar{x}^2}.$$

The values obtained using the coordinates presented above can be summarized as follows:

Time t (s)	$\bar{x}$ (cm$_i$)	$\bar{y}$ (cm$_i$)	Δx (cm$_i$)	$\bar{d}$ (cm$_i$)	$\bar{d}^*$ (cm$_i$)	$\bar{z}$ (cm$_i$)
1	−1.80	2.13	3.01	3.04	2.18	1.22
2	−0.94	2.66	2.94	3.14	1.68	1.39
3	−3.83	3.97	3.08	5.63	4.00	1.16

The movement of the head of the fish between two successive time intervals t and $t + 1$ (M_t', cm·s^{-1}) was estimated as

$$M_t' = (S_t \cdot m_t')/\Delta\bar{x}_t$$

where $\Delta\bar{x}_t$ (cm$_i$) is the average apparent displacement of the target at time t and $t + 1$, s_t (cm) is the optical axes separation, and m_t' (cm$_i$) is the movement of the target between t and $t + 1$ in image units.

$\Delta\bar{x}_t$ was estimated as

$$\Delta\bar{x}_t = (\Delta x_t + \Delta x_{t+1})/2.$$

S_t was estimated using the empirical relationship derived during the calibration for field conditions:

$$S_t = (-0.065 \cdot (\Delta\bar{x}_t)^2) + (1.02 \cdot \Delta\bar{x}_t) + 5.39.$$

m_t' was estimated as

$$m_t' = \sqrt{[(\bar{x}_{t+1} - \bar{x}_t)^2 + (\bar{y}_{t+1} - \bar{y}_t)^2 + (\bar{z}_{t+1} - \bar{z}_t)^2]}.$$

The speed of the head of the fish (VH$_t'$, cm·s^{-1}) at time t was estimated as

$$\mathrm{VH}_t' = m_t' \cdot \Delta t^{-1}$$

where Δt is the time interval between t and $t + 1$ (i.e. generally 1 s). In summary:

Time t (s)	$\Delta\bar{x}_t$ (cm$_i$)	m_t' (cm$_i$)	$M_t' = \mathrm{VH}_t'$ (cm)
1	2.98	1.03	2.73
2	3.01	3.18	8.32
3	—	—	—

Modèles empiriques de la production annuelle et du rapport *P/B* d'invertébrés benthiques d'eau courante

Antoine Morin et Nathalie Bourassa

Institut de biologie Ottawa-Carleton, Département de biologie, Université d'Ottawa, Ottawa (Ontario) K1N 6N5, Canada

Morin, A. et N. Bourassa. 1992. Modèles empiriques de la production annuelle et du rapport *P/B* d'invertébrés benthiques d'eau courante. Can. J. Fish. Aquat. Sci. 49: 532–539.

Des données publiées sur la productivité d'invertébrés d'eau courante sont réanalysées par régression multiple afin de (1) quantifier la relation existant entre la productivité (*P*, en grammes de masse sèche par mètre carré par an), la biomasse (*B*, en grammes de masse sèche par mètre carré) la masse individuelle (*M*, en grammes de masse sèche) et la température moyenne annuelle de l'eau (*T*, en degrés Celsius), (2) de comparer la productivité des principaux groupes taxonomiques et (3) de comparer cette relation à celles observées pour des populations d'invertébrés d'autres écosystèmes aquatiques. La relation $P = 0,18\ B^{1,01}\ M^{-0,34}\ 10^{0,037T}$ explique 87 % de la variabilité de log *P* entre les 291 populations d'invertébrés lotiques analysées. Des différences significatives ont été détectées entre les principaux groupes taxonomiques, mais ces différences n'expliquent qu'environ 4 % de la variabilité de log *P*. La productivité des invertébrés de lacs et d'eau courante est très similaire lorsque corrigée pour l'effet de la biomasse, la masse individuelle et de la température. Contrairement à ce qui a été observé pour les lacs, la productivité est reliée linéairement à la biomasse pour les invertébrés vivant en ruisseaux et rivières. La comparaison de la relation pour les écosystèmes d'eau courante, de lac et marin suggère que les populations d'invertébrés marins sont moins productives que les populations dulcicoles.

Published data on secondary production of running water invertebrates are analyzed by multiple regression to quantify the relationship between productivity (*P*, in grams dry mass per square metre per year) and biomass (B, in grams dry mass per square metre), mean individual mass (*M*, in grams dry mass), and annual mean water temperature (*T*, in degrees Celsius) to compare productivity of major taxonomic groups and to compare to invertebrate populations from other aquatic ecosystems. The equation $P = 0.18\ B^{1.01}\ M^{-0.34}\ 10^{0.037T}$ explains 87% of the variability in log *P* in the 291 lotic invertebrate populations analyzed. Significant differences were detected among major taxonomic groups, but these differences account for only about 4% of the variability in log *P*. Once the effect of biomass, mean individual mass and water temperature are taken into account, productivity of lake and stream invertebrate populations is quite similar, although productivity is a linear function of biomass in streams and not in lakes. Comparison of models for running waters, lake and marine ecosystems suggests that marine invertebrates are less productive than freshwater populations.

Reçu le 13 juin 1991
Accepté le 4 octobre 1991
(JB081)

Received June 13, 1991
Accepted October 4, 1991

L'utilisation rationnelle des ressources naturelles renouvelables présuppose une connaissance des facteurs qui affectent leur productivité. Les invertébrés vivant dans les écosystèmes lotiques influencent les transferts d'énergie des producteurs primaires et du matériel allochtone vers les poissons, ainsi que le recyclage et la rétention des éléments nutritifs. Leur productivité est donc un aspect important à considérer lors de l'aménagement des ruisseaux et rivières ou de leur utilisation à des fins sportives et récréatives.

L'étude de la productivité des populations et des communautés naturelles d'invertébrés est toutefois compliquée et coûteuse car elle implique un échantillonnage serré et une estimation de plusieurs paramètres démographiques (Benke 1984; Rigler et Downing 1984). Pour contourner ces problèmes logistiques, plusieurs chercheurs ont suggéré des alternatives. Puisqu'il semble exister une relation entre le rapport de la production à la biomasse (*P/B*) et des caractéristiques du cycle vital des organismes, Mann (1969) et Waters (1977) ont suggéré que la productivité pourrait être grossièrement estimée par le produit de la biomasse moyenne annuelle et du rapport *P/B* présumé en fonction du cycle vital. Cette approche a été développée par Banse et Mosher (1980) qui ont produit une relation empirique entre le rapport *P/B* et la masse individuelle à maturité de plusieurs groupes d'organismes.

Plus récemment, Plante et Downing (1989) ont développé un modèle empirique reliant la production annuelle d'invertébrés benthiques et planctoniques lacustres à leur biomasse, leur masse individuelle maximale et à la température moyenne annuelle. Brey (1990) a suivi une approche similaire en reliant la productivité de macroinvertébrés benthiques marins et lacustres à la biomasse moyenne annuelle et à la masse individuelle moyenne. Plante et Downing (1989) n'ont pas analysé de données sur les invertébrés vivant en eau courante, prétextant des différences radicales entre les environnements lotiques et lentiques. Pour sa part, Brey (1990) a exclu les données sur les insectes de son analyse, prétextant un cycle vital unique parmi les macroinvertébrés benthiques. L'effet de la température sur la productivité n'a pas été analysé par Brey. Il n'existe donc pas de modèle empirique reliant la productivité des insectes lotiques à la biomasse, la masse individuelle et à la température. De plus, si l'on accepte les arguments de Plante et Downing (1989) et de Brey (1990), les modèles publiés ne devraient pas être utilisés pour ces organismes.

Nous présentons ici une réanalyse des données publiées visant à quantifier la relation entre la productivité de macroinvertébrés lotiques, d'une part, et la biomasse moyenne annuelle, la masse individuelle moyenne et la température moyenne annuelle d'autre part. Le but de cette analyse est de produire une équation générale permettant d'estimer la productivité des invertébrés lotiques, et de comparer la productivité de divers groupes taxonomiques afin de déterminer s'il est préférable d'utiliser plusieurs équations spécifiques plutôt qu'une équation générale. La relation entre la productivité, la biomasse, la masse moyenne et la température pour les invertébrés d'eau courante est par la suite comparée aux relations décrites par Brey (1990) et Plante et Downing (1989) afin de déterminer s'il existe des différences de productivité et de rapport P/B entre les invertébrés benthiques des milieux lotiques, lacustres et marins.

Méthodes

Récolte des données

Les données de productivité secondaire (P, en grammes de masse sèche (MS) par mètre carré par an), de biomasse moyenne annuelle (B, en grammes de MS par mètre carré) et de masse individuelle moyenne (M, en grammes de MS) ont été récoltées dans la littérature en parcourant les volumes publiés entre 1979 et 1990 de *Aquatic Insects, Canadian Journal of Fisheries and Aquatic Sciences, Canadian Journal of Zoology, Ecological Monograph, Ecology, Freshwater Biology, Holarctic Ecology, Hydrobiologia, Journal of the North American Benthological Society* et *Limnology and Oceanography*. Seuls les estimés basés sur un échantillonnage couvrant toute l'année et accompagnés de données de température de l'eau (T, en degrés Celsius) ont été retenus. Les estimés de production obtenus en multipliant la biomasse moyenne par le rapport P/B mesuré pour une autre population ont également été rejetés. Lorsque nécessaire, les données exprimées en unités de masse humide ou de masse sèche sans les cendres ont été converties en unités de masse sèche en utilisant les facteurs de conversion rapportés par les auteurs ou ceux de Hamill (1975). La masse individuelle moyenne a été calculée en divisant la biomasse moyenne annuelle par la densité moyenne annuelle. Les données de productivité, de biomasse et de masse sèche pour les Mollusques excluent la coquille. La température moyenne annuelle de l'eau, lorsqu'elle n'était pas donnée dans les articles, a été calculée à partir des données présentées en tableau ou figure en faisant la moyenne des températures données, pondérée par l'intervalle de temps correspondant à chaque lecture.

Analyses statistiques

La relation entre la productivité et la biomasse, la masse individuelle moyenne et la température de l'eau a d'abord été quantifiée à partir de l'ensemble des données en estimant les coefficients d'un modèle de régression linéaire multiple de la forme

$$(1)\quad \log_{10} P = a + b \log_{10} B + c \log_{10} M + dT.$$

La transformation logarithmique opérée sur P, B et M a permis de linéariser la relation entre ces variables et de stabiliser la variance de l'erreur résiduelle.

Par la suite, l'analyse par régression multiple a été répétée séparément pour chacun des principaux groupes taxonomiques. Les régressions pour chaque groupe ont été comparées entre elles par analyse de covariance (ANCOVA) afin de déterminer si les coefficients (a, b, c et d dans l'Eq. 1) varient significativement entre les groupes. Les régressions pour chaque groupe ont également été comparées individuellement à la régression estimée sur l'ensemble des données afin de déterminer si le modèle général peut être appliqué à des groupes particuliers sans biaiser significativement les valeurs prédites. Ces comparaisons ont été effectuées par un test de F (avec 4 degrés de liberté pour le numérateur et $n - 4$ degrés de liberté pour le dénominateur) sur le rapport

$$(2)\quad F = \frac{(SC_{\text{Taxon}} - SC_{\text{Général}})}{4s^2_{\text{Taxon}}}$$

où n est le nombre d'observations pour le groupe taxonomique pour lequel l'équation de régression est comparée à l'équation générale, SC_{Taxon} et $SC_{\text{Général}}$ sont respectivement la somme des carrés des écarts attribuables à la régression spécifique et à la régression générale lorsqu'appliquée seulement aux données du groupe taxonomique qui est comparé, et s^2_{Taxon} est la variance de l'erreur résiduelle de la régression pour le taxon comparé.

Résultats

Description de l'ensemble de données

Les analyses sont basées sur 291 estimés de productivité provenant de 35 publications portant sur des populations de 32 ruisseaux et rivières, principalement des régions tempérées de l'hémisphère nord (tableau 1). La très grande majorité (272/291) des estimés de production annuelle recueillis ont été calculés par la méthode des fréquences de tailles (Hynes-Hamilton; Benke 1984; Rigler et Downing 1984). Le tableau 2 présente un sommaire des valeurs observées.

Modèle général

L'analyse par régression multiple de l'ensemble des données révèle que la productivité des invertébrés d'eau courante est positivement reliée à leur biomasse et à la température de l'eau, et négativement reliée à la masse individuelle moyenne. L'équation de régression

$$(3)\quad \log P = -0{,}75 + 1{,}01 \log B - 0{,}34 \log M + 0{,}037\, T$$
$$n = 291;\ R^2 = 0{,}87;\ \text{RMS} = 0{,}117$$

explique 87 % de la variabilité observée entre les valeurs de log P (fig. 1). Des trois variables indépendantes, la biomasse annuelle moyenne est celle qui est le plus fortement reliée à la productivité (corrélation partielle de 0,93; $p < 0{,}0001$) et explique à elle seule près de 79 % de la variabilité de log P. La masse individuelle moyenne (corrélation partielle de $-0{,}63$; $p < 0{,}0001$) et la température corrélation partielle de 0,47; $p < 0{,}0001$) expliquent respectivement 8,6 et 3,8 % de la variabilité de log P dans cet ensemble de données. Les valeurs observées varient en moyenne d'un facteur de 2,2 des valeurs prédites, mais dans les pires des cas elles peuvent différer des valeurs prédites d'un facteur de 10.

Comparaison des groupes taxonomiques

La comparaison de la productivité observée et de celle prédite par le modèle général (fig. 2) illustre les fortes corrélations entre les valeurs observées et prédites. Cependant elle suggère qu'il existe des différences de productivité entre certains taxa qui ne peuvent être expliquées par des différences de biomasse, de masse moyenne ou de température de l'eau. En moyenne, le modèle général sous-estime la productivité des Diptères (moyenne des erreurs résiduelles (RMS) = 0,09; test de t, p = 0,017) et des Mégaloptères (moyenne = 0,30; p = 0,018); et il surestime la productivité des Mollusques (moyenne = 0,76;

TABLEAU 1. Liste des sites pour lesquels les données de productivité ont été retenues. Le nombre d'estimés de productivité (n) et la température moyenne annuelle de l'eau sont donnés pour chaque site.

Site	Coordonnées	n	Température (°C)	Référence(s)
Anna River	37°N, 77°O	1	18,4	Parker et Voshell 1983
Ball Creek	35°N, 83°O	43	8,3	Huryn et Wallace 1985, 1987a, 1987b, 1988
Black Creek	32°N, 83°O	1	19,5	Benke et Parsons 1990
Blanco	29°N, 98°O	1	21,9	Short et al. 1987
Buzzard	37°N, 76°O	19	16,0	Roeding et Smock 1989
Cedar Creek	33°N, 81°O	32	17,6	Smock et al. 1985
Dryman Fork	36°N, 86°O	24	9,5	Ross et Wallace 1983
Fonstrup Baek	58°N, 12°E	1	9,1	Iversen 1980
Grabia River	52°N, 19°O	14	9,0	Grzybkowska et Witczak 1990
Guadelupe	29°N, 98°O	1	20,5	Short et al. 1987
Hidden	43°S, 170°E	1	10,0	Collier et Winterbourn 1990
Honey	29°N, 98°O	1	21,4	Short et al. 1987
L'Achigan	46°N, 74°O	2	8,4	Lauzon et Harper 1986
Little Shultz	33°N, 87°O	2	17,3	Richardson et al. 1988
Moat Feeder	51°N, 3°O	1	10,1	Lazim et Learner 1986
Ogeechee	32°N, 83°O	2	19,3	Benke et Parsons 1990
Ottawa River	46°N, 73°O	23	9,0	Hamill et al. 1979
Palau	7°N, 134°E	9	25,5	Bright 1982
River Ely	51°N, 3°O	1	11,8	Murphy et Learner 1982
Rold Kilde	56°N, 9°E	2	7,5	Iversen et Jessen 1977
Rose Creek	33°N, 83°O	2	17,5	Freeman et Wallace 1984
Samson	49°N, 4°E	4	9,4	Rosillon 1986
San Marcos	29°N, 98°O	1	22,2	Short et al. 1987
Satilla	31°N, 82°O	52	19,0	Benke et al. 1984
Savannah	32°N, 81°O	17	16,5	Cudney et Wallace 1980
Steep	43°S, 170°E	1	9,5	Collier et Winterbourn 1990
Suspect	43°S, 170°E	1	10,5	Collier et Winterbourn 1990
Sycamore	33°N, 110°O	7	18,5	Jackson et Fisher 1986
Tallulah	34°N, 83°O	6	11,0	Benke et Wallace 1980
Toilet	43°S, 170°E	1	11,0	Collier et Winterbourn 1990
Valley Creek	45°N, 92°O	18	9,1	Waters et Hokenstrom 1980; Mackay et Waters 1986
Valley River	51°N, 100°O	1	10,0	Giberson et Galloway 1985

TABLEAU 2. Minima, maxima et médianes des valeurs de biomasse, de masse individuelle moyenne, de température de l'eau et de productivité.

Variable	Unités	Minimum	Maximum	Médiane
Biomasse	g MS·m^{-2}	0,0006	45,7	0,041
Masse individuelle	mg MS	0,0008	186	0,35
Température	°C	7	25,5	16
Productivité	g MS·m^{-2}·an^{-1}	0,003	138	0,4

$p < 0{,}0001$) et des Coléoptères (moyenne = 0,45; p = 0,0014).

La relation entre la productivité et la biomasse, la masse moyenne et la température varie entre les taxa (tableau 3). Les coefficients de régression associés à la biomasse, la masse individuelle et la température varient significativement entre les principaux groupes taxonomiques (ANCOVA; $F = 6{,}45$; 27 dl, 259 dl; $p < 0{,}0001$). Les différences de pentes et d'ordonnées à l'origine entre les groupes expliquent environ 30 % de la variabilité résiduelle du modèle général, ce qui équivaut à environ 4 % de la variabilité totale de log P. Toutefois, le faible effectif de la plupart des groupes n'a pas permis d'estimer précisément les coefficients des modèles pour ces taxa.

Non seulement les régression pour les différents taxa diffèrent entre elles, mais plusieurs diffèrent significativement de la régression sur l'ensemble des données: celles pour les Coléoptères ($F = 526$; 4 dl, 1 dl; $P = 0{,}03$), les Diptères ($F = 2{,}7$; 4 dl, 66 dl; P = 0.04), les Odonates ($F = 16{,}5$; 4 dl, 6 dl; $p = 0{,}002$), les Plécoptères ($F = 5{,}9$; 4 dl, 9 dl; $p = 0{,}01$) et les Trichoptères ($F = 7{,}6$; 4 dl, 104 dl; $p < 0{,}0001$).

La précision des valeurs prédites par les équations de régression varie significativement entre les principaux groupes taxonomiques. Tel que suggéré par la dispersion des valeurs observées par rapport aux valeurs prédites à la fig. 2, la variance de l'erreur résiduelle des régressions pour les Diptères (0,196), les Éphéméroptères (0,147) est nettement supérieure à celles observées pour les autres groupes. Un test de Kruskal–Wallis effectué sur les valeurs absolues des erreurs résiduelles des 10 modèles présentés au tableau 3 a révélé une différence significative de précision entre les taxa (chi-carré = 74; 9 dl; $p < 0{,}0001$).

Discussion

Biomasse

La productivité des invertébrés lotiques est directement proportionnelle à leur biomasse moyenne annuelle. Le coefficient associé à la biomasse dans le modèle général (1,01) ne diffère pas significativement de 1,0, ce qui implique que la production des invertébrés est linéairement reliée à leur biomasse et que le rapport P/B n'est pas influencé par la biomasse. Ce résultat est identique à celui de Brey (1990) qui

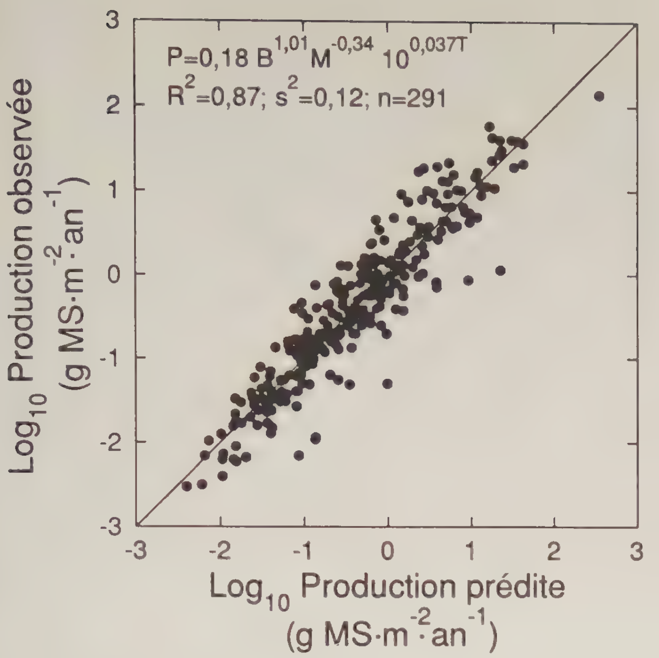


FIG. 1. Production observée et prédite par le modèle général pour les invertébrés lotiques (Eq. 3). La diagonale est la droite 1:1.

a également obtenu un coefficient de 1,01 pour la biomasse d'invertébrés benthiques marins et lacustres. Banse et Mosher (1980) ont pour leur part dénoté l'absence de relation entre le rapport *P*/*B* et la biomasse moyenne, ce qui implique aussi que la production est directement proportionnelle à la biomasse. Dans son analyse, Humphreys (1981) a observé que le coefficient reliant la productivité (log *P*) à un indice de la densité des populations corrigé pour leur capacité métabolique (log I_m, i_m étant calculé comme $BM^{-0,75}$) était de 0,68 pour les invertébrés terrestres et aquatiques, ce qui impliquerait que la productivité serait proportionnelle à $B^{0,68}$. Une réanalyse des données de Humphreys (1981) par régression multiple donne, après conversion d'unités (1 kcal ≈ 0,2 g MS; 1 g de masse fraîche ≈ 0,2 g MS) :

$$(4) \quad \log P = -0.12 + 1.15 \log B - 0.25 \log M' \qquad n = 32;\ R^2 = 0{,}83;\ \mathrm{RMS} = 0{,}192$$

où M' est la masse sèche maximale (grammes MS), et où le coefficient pour la biomasse ne diffère pas significativement de 1,0. Plante et Downing (1989) ont cependant observé une valeur significativement plus faible (0,79) pour des invertébrés lacustres, ce qui implique une relation non linéaire entre la productivité ou le rapport *P*/*B* et la biomasse. La relation entre la productivité et la biomasse semble donc être différente pour les invertébrés lacustres.

Masse individuelle

Pour une biomasse et une température donnée, la productivité des invertébrés lotiques diminue avec une augmentation de la taille ($P \propto M^{-0,34}$). Le coefficient associé à la masse individuelle (IC 95 % : −0,38 à −0,30) est significativement plus petit que la valeur théorique de −0,25 communément observée pour les taux métaboliques spécifiques (Peters 1983). Cependant, compte tenu de l'erreur associée aux coefficients de régression, la valeur observée ne diffère pas significativement des coefficients estimés par Banse et Mosher (−0,34 pour la masse moyenne des adultes, IC 95 % : −0,41 à −0,28) et Brey (−0,27, IC 95 % : −0,31 à −0,24), ni de la valeur de −0,25 (MS maximale, IC 95 % : −0,37 à −0,13) recalculée à partir des données de Humphreys. Par contre, nos résultats contredisent la généralisation de Plante et Downing (1989), basée sur leur analyse de la relation entre la production et la masse individuelle maximale ($M_{\max}$ en milligrammes MS, exposant = −0,16), et selon laquelle l'exposant associé à la masse individuelle est plus grand que −0,25 pour les invertébrés aquatiques.

L'utilisation de $M_{\max}$ au lieu de M dans le modèle de régression de Plante et Downing (1989) pour les invertébrés de lac semble expliquer la différence d'exposant pour la masse individuelle entre les lacs et les ruisseaux. L'analyse d'un sous-ensemble des données de Plante et Downing (1989) pour lesquelles nous avons pu obtenir la masse individuelle moyenne révèle que la production d'invertébrés de lacs peut être décrite par les relations

$$(5) \quad \log P = 0{,}24 + 0{,}82 \log B - 0{,}17 \log M_{\max} + 0{,}044\,T \qquad n = 53;\ R^2 = 0{,}70;\ \mathrm{RMS} = 0{,}173$$

$$(6) \quad \log P = -1{,}25 + 0{,}85 \log B - 0{,}34 \log M + 0{,}059\,T \qquad n = 53;\ R^2 = 0{,}77;\ \mathrm{RMS} = 0{,}135.$$

Dans la régression multiple sur ce sous-ensemble de données l'utilisation de M au lieu de $M_{\max}$ permet d'expliquer 7 % de plus de la variabilité de log *P*, et abaisse le coefficient associé à la masse individuelle (IC 95 % : −0,46 à 0,26) à la valeur observée pour les invertébrés lotiques.

Température

L'équation 3 indique que la production augmente avec la température et est proportionnelle à $10^{0,037T}$, ce qui se traduit par un Q_{10} d'environ 2,3. L'effet de la température sur la productivité est plus élevé que celui observé pour les taux spécifiques de croissance des larves de simulies (Q_{10} = 1,4; Morin et al. 1988b), mais similaire à celui observé pour leur taux d'ingestion (Q_{10} = 2,2; Morin et al. 1988a). Plante et Downing (1989) rapportent un effet significativement plus marqué de la température (Q_{10} = 3,2) sur la production des invertébrés lacustres.

Rapport *P*/*B*

L'équation 3 permet de calculer les rapports *P*/*B* attendus en fonction de la masse individuelle moyenne et de la température de l'eau (fig. 3). Le rapport *P*/*B* augmente avec un accroissement de la température et diminue avec une augmentation de la masse individuelle moyenne. Les forts rapports *P*/*B* pour les petits organismes vivant dans des eaux chaudes décrits par la fig. 3 s'accordent assez bien avec les valeurs observées par Benke et Parsons (1990) pour des simulies de rivières du sud est des États-Unis (37–85).

Comparaison des groupes taxonomiques

Comme Brey (1990) nous avons détecté des différences de productivité entre les taxa qui ne peuvent être expliquées par la biomasse, la masse individuelle ou la température. La comparaison des modèles estimés pour les principaux groupes taxonomiques a permis de détecter des différences statistiquement significatives, mais relativement peu importantes; ces différences entre les groupes n'expliquent en effet qu'environ 4 % de la variabilité totale de log *P*, comparées aux 87 % expliquées par la relation générale. L'utilisation des modèles spécifiques permet donc de prédire un peu plus précisément la production

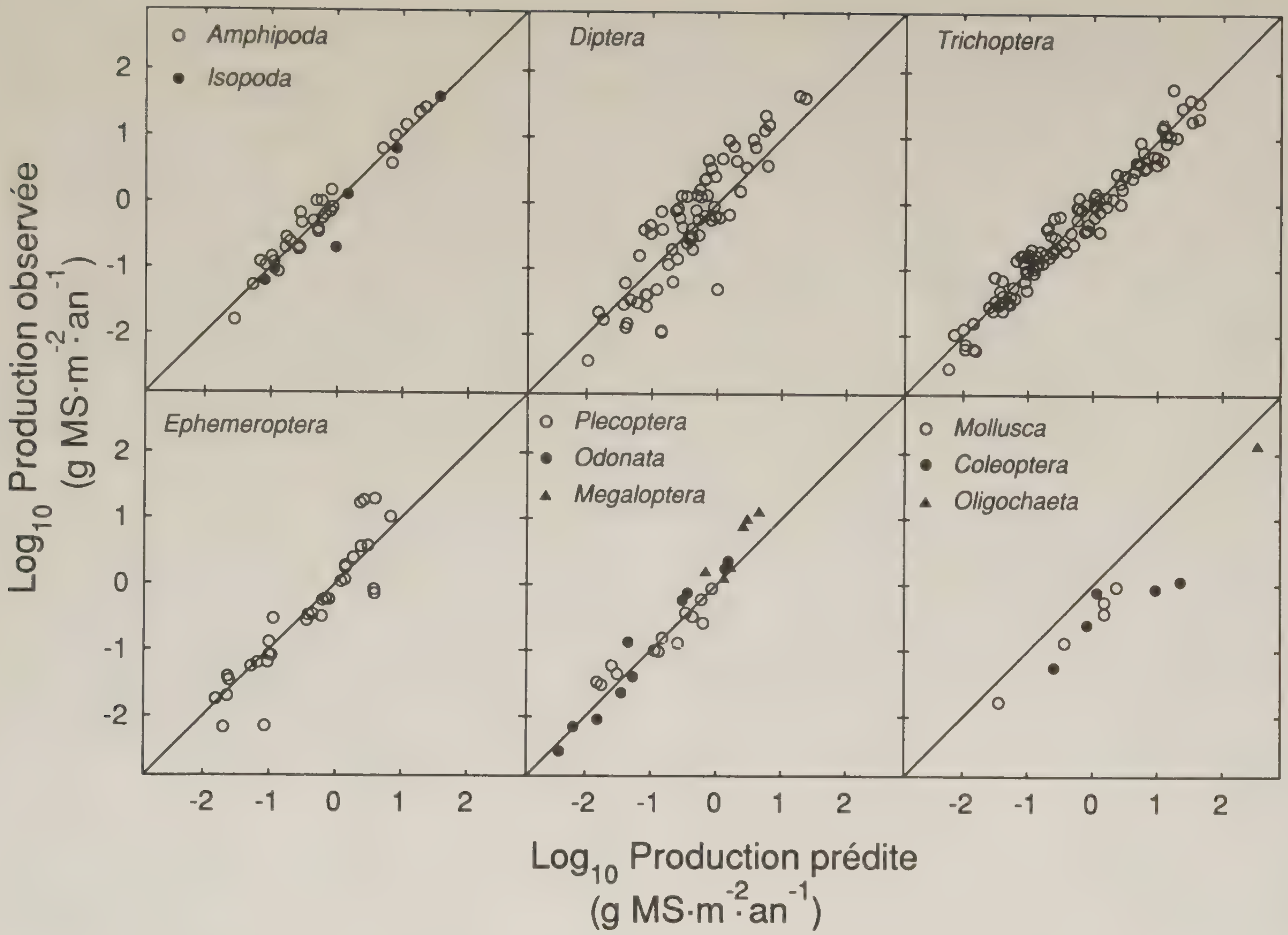


FIG. 2. Production observée pour différents taxa en fonction de la production prédite par le modèle général (Eq. 3).

que l'emploi d'une seule équation pour tous les groupes, mais surtout d'éliminer le biais du modèle général pour certains groupes.

Il est cependant possible que les différences détectées reflètent des différences entre études ou sites plutôt que des différences fondamentales entre les groupes taxonomiques. Comme l'ensemble des données est tiré d'un nombre relativement restreint d'études, et que les données pour les différents groupes taxonomiques ne proviennent typiquement pas des mêmes sites, il est possible que les différences détectées entre les groupes soient causées par d'autres facteurs que la biomasse, la masse individuelle, la température ou le taxa. Des données supplémentaires, idéalement récoltées pour chacun des groupes dans les mêmes conditions et les mêmes sites, permettraient de trancher entre ces deux explications aux différences intergroupes observées.

Quoi qu'il en soit, nos résultats ne supportent pas les réserves de Brey (1990) quant à l'effet des différences de cycle vital sur la productivité. Nous n'avons pas observé de différences marquées de productivité (corrigée pour B, M et T) entre les Crustacés et les Insectes. À défaut de modèles spécifiques plus précis, l'équation 3 peut être utilisée pour tous les groupes d'invertébrés lotiques.

Comparaison entre les écosystèmes aquatiques

Contrairement à ce que croyaient Plante et Downing (1989), les différences marquées des conditions physiques entre les lacs et les eaux courantes semblent avoir peu d'effet sur la productivité des organismes. La productivité des populations d'invertébrés de lac (benthiques et planctoniques) peut être, en moyenne, adéquatement prédite par l'emploi de l'Eq. 3 (fig. 4) mais avec une sous-estimation des productivités les plus faibles et une surestimation des productivités les plus élevées. La comparaison des Eq. 3 et 6 suggère que c'est principalement la relation entre P et B qui varie entre ces deux habitats. La différence pourrait également être expliquée par une différence entre les estimés utilisés pour le modèle en lac et celui en eau courante. Les données analysées ici ont presque toutes été obtenues par la méthode des fréquences de tailles (Hynes-Hamilton), alors que les données utilisées pour estimer le modèle pour les lacs ont majoritairement été obtenues par d'autre méthodes, considérées plus exactes (Morin et al. 1987). Cependant, Plante et Downing (1990) n'ont pu détecter de biais des diverses méthodes d'estimation de la production dans leur analyse de la variabilité résiduelle autour des valeur prédites par leur modèle pour les lacs. Il est donc peu probable que les faibles différences entre les lacs et les eaux courantes soient causées par une différence de méthodes utilisées.

Par contre, le modèle de Brey (1990), estimé principalement à partir de données d'invertébrés marins, implique que le rapport P/B de ces organismes est typiquement plus bas que celui observé pour les invertébrés duplicoles (fig. 5). Cette différence entre les milieux marins et dulcicoles pourrait être causée par des différences entre les groupes taxonomiques étudiés par Brey (son ensemble de données est dominé par les Mollusques), TABLEAU 3. Modèles de régression multiple estimés pour les principaux groupes taxonomiques. Coefficients (et erreur standard, ES) du modèle de régression multiple entre le logarithme de la productivité ($g\ MS \cdot m^{-2} \cdot an^{-1}$) et le logarithme de la biomasse moyenne annuelle ($\log B$, $g\ MS \cdot m^{-2}$), le logarithme de la masse individuelle moyenne ($\log M$, g MS) et la température moyenne annuelle de l'eau (T, °C). Le nombre d'observations (n), le coefficient de détermination multiple (R^2) et la variance de l'erreur résiduelle (RMS) sont également présentés pour chaque régression. Les astérisques indiquent la probabilité que le coefficient de régression partiel soit égal à zéro (test de t :^{ns} $p >$,05, *0,05 $> p >$ 0,01, **0,01 $> p >$ 0,001; ***$p <$ 0,001).

Modèle	n	Intercept (ES)	log B (ES)	log M (ES)	T (ES)	R^2	RMS
Général	291	−0,75	1,01***	−0,34***	0,037***	0,87	0,117
		(0,09)	(0,02)	(0,02)	(0,004)		
Amphipoda	31	0,60	1,02***	0,02^{ns}	0,016^{ns}	0,96	0,025
		(0,53)	(0,04)	(0,16)	(0,018)		
Coleoptera	5	1,80	0,94*	0,24^{ns}	−0,015^{ns}	0,99	0,001
		(0,60)	(0,02)	(0,08)	(0,018)		
Diptera	67	−1,07	1,12***	−0,38***	0,062***	0,79	0,196
		(0,37)	(0,09)	(0,08)	(0,014)		
Ephemeroptera	35	−0,26	1,11***	−0,25^{ns}	0,035*	0,85	0,147
		(0,50)	(0,09)	(0,13)	(0,013)		
Isopoda	6	−0,43	1,05*	−0,29^{ns}	0,017^{ns}	0,98	0,080
		(0,42)	(0,13)	(0,14)	(0,020)		
Megaloptera	6	−3,90	1,15^{ns}	−0,44^{ns}	0,198^{ns}	0,95	0,020
		(8,40)	(0,34)	(1,21)	(0,313)		
Mollusca	5	3,90	−0,40^{ns}	0,89^{ns}	−0,120^{ns}	0,91	0,105
		(4,41)	(0,88)	(0,85)	(0,143)		
Odonata	10	−0,01	0,97***	−0,01^{ns}	0,035**	0,99	0,008
		(0,21)	(0,04)	(0,06)	(0,009)		
Plecoptera	13	−0,62	0,69***	−0,16*	0,033**	0,94	0,018
		(0,30)	(0,07)	(0,06)	(0,010)		
Trichoptera	108	−0,18	1,00***	−0,19***	0,027***	0,96	0,035
		(0,12)	(0,02)	(0,03)	(0,004)		

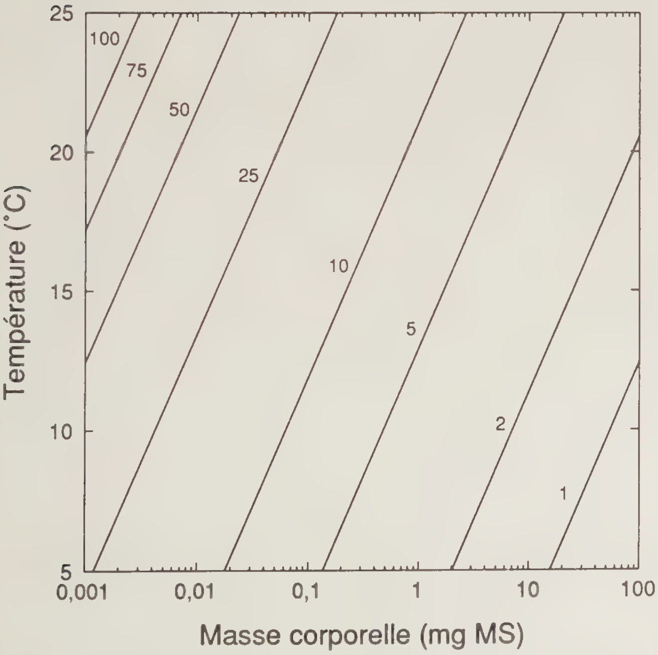


FIG. 3. Rapport P/B d'invertébrés d'eau courante en fonction de la température de l'eau et de la masse individuelle moyenne. Les valeurs sont calculées à partir de l'Eq. 3.

ou partiellement par une différence de température. Les valeurs de P/B en lac et en ruisseau illustrées à la fig. 5 ont été calculées pour une température de 14 °C, qui correspond à la valeur moyenne des données de Plante et Downing (1989) et de celles

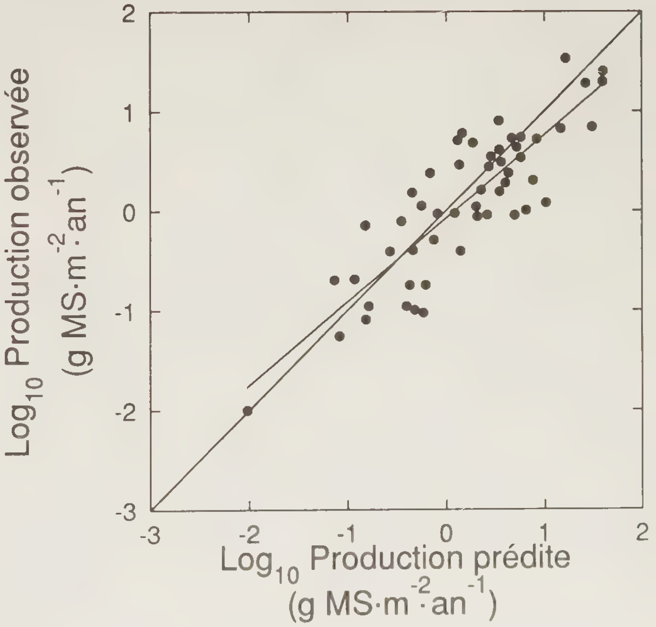


FIG. 4. Comparaison de la productivité en lac et en eau courante. Production observée pour le sous-ensemble des données sur les invertébrés de lac de Downing et Plante (1989) pour lesquelles nous avons pu estimer la masse individuelle moyenne, en fonction de la production prédite par le modèle général pour les eaux courantes (Eq. 3). La courte droite est la droite de régression $\log P_{observée} = 0{,}06 + 0{,}83 \log P_{prédite}$ ($n = 53$). La pente de cette droite est significativement plus petite que 1,0 ($p = 0{,}013$).

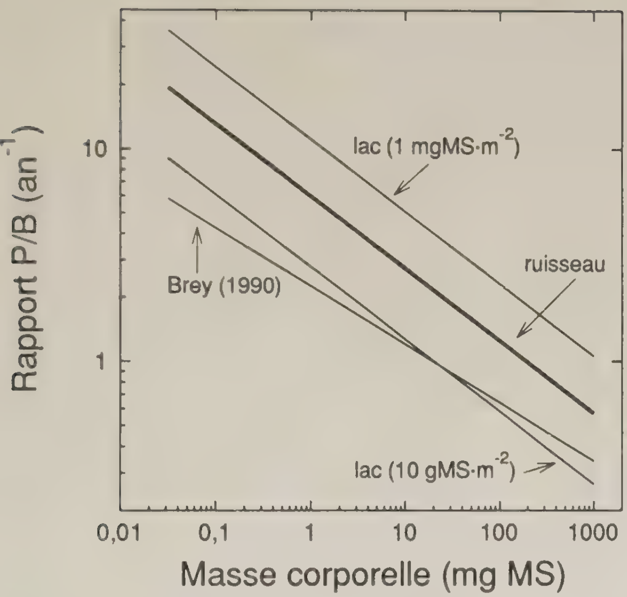


FIG. 5. Relation entre le rapport P/B et la masse individuelle moyenne dans les lacs, les ruisseaux et pour les données de Brey (1990) comprenant majoritairement des invertébrés marins. Les droites pour les ruisseaux et les lacs ont été calculées à partir des Eq. 3 et 6 respectivement, pour une température de 14 °C. Le rapport P/B étant influencé par la biomasse en lac, la relation est illustrée pour une biomasse faible (1 mg MS·m^{-2}) et pour une biomasse élevée (10 g MS·m^{-2}).

analysées ici. En supposant un Q_{10} de 2,0, la différence de rapport P/B entre les ruisseau et les données de Brey correspond à environ 15 °C. Il faudrait que la température moyenne annuelle pour les sites d'où proviennent ces données soit d'environ 0 °C pour ramener la droite au niveau de celle des eaux courantes. Comme la majorité des données de Brey proviennent de la zone littorale dans des régions tempérées, il est peu probable que la différence soit entièrement attribuable à une différence de température. Une analyse plus poussée, incluant l'effet de la température, est néanmoins souhaitable afin de déterminer si les organismes marins sont réellement moins productifs que les organismes dulcicoles.

Précision des estimés et amélioration possibles

L'ajustement des valeurs observées aux équations de régression du type de l'Eq. 3 est très bon, compte tenu des erreurs de mesure de la biomasse et de la productivité de populations naturelles (Morin et al. 1987). Il est cependant sans doute possible d'améliorer la précision des modèles empiriques. Plante et Downing (1989) ont identifié plusieurs variables qui peuvent expliquer une fraction significative de la variabilité résiduelle au modèle qu'ils présentent pour les lacs. La plupart de ces variables peuvent être considérées comme des indices de la productivité primaire. Il est vraisemblable que la disponibilité de nourriture puisse expliquer une bonne partie de la variabilité restante pour les invertébrés lotiques. Le gain de précision devrait cependant être comparé au coût de mesure de variables supplémentaires.

Un indice de la température légèrement différent de celui utilisé ici pourrait peut-être améliorer la précision des prédictions sans pour autant augmenter le coût de mesure. Benke et Parsons (1990) mentionnent que le rapport P/B annuel de populations de simulies varie substantiellement entre sites ayant une température moyenne annuelle semblable. Il explique cette différence par le fait que les populations n'atteignent pas leur biomasse maximale au même moment dans l'année, et donc que la période la plus productive pour ces populations a lieu à des températures différentes. Ce type de situation ne peut être accommodé en utilisant la température moyenne annuelle comme indice de la température à laquelle la biomasse productive a été exposée en moyenne. Par contre, si la température moyenne annuelle est pondérée par la biomasse pour créer un indice de la température T' calculé, par exemple, comme

$$(7)\quad T' = \frac{\sum_{i=1}^{n} B_i T_i}{\sum_{i=1}^{n} B_i}$$

où B et T sont la biomasse et la température observée à chaque date d'échantillonnage i, alors cet indice tiendrait compte de la phénologie de la production. Un tel indice permettrait potentiellement de prédire correctement la production dans des situations comme celles décrites par Benke et Parsons et où des modèles du type de l'Eq. 3 seraient inadéquats.

Remerciements

Cette étude a été rendue possible grâce au support financier du Conseil de Recherches en Sciences Naturelles et en Génie du Canada. Céline Plante nous a généreusement donné accès à son ensemble de données. Nous les en remercions.

Références

BANSE, K. ET S. MOSHER. 1980. Adult body mass and annual production/biomass relationships in field populations. Ecol. Monogr. 50: 355–379.

BENKE, A. C. 1984. Secondary production of aquatic insects, p. 289–323 *Dans* V. H. Resh et D. M. Rosenberg [ed.] Ecology of aquatic insects. Prager Publisher, New York, NY.

BENKE, A. C. ET K. A. PARSONS. 1990. Modelling black fly production dynamics in blackwater streams. Freshwater Biol. 24: 167–180.

BENKE, A. C., T. C. VAN ARSDALL JR. ET D. M. GILLESPIE. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecol. Monogr. 54: 25–63.

BENKE, A. C. ET J. B. WALLACE. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology 61: 108–118.

BREY, T. 1990. Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. Meeresforschung 32: 329–343.

BRIGHT, G. R. 1982. Secondary benthic production in a tropical island stream. Limnol. Oceanogr. 27: 472–480.

COLLIER, K. J. ET M. J. WINTERBOURN. 1990. Population dynamics and feeding of mayfly larvae in some acid and alkaline New Zealand streams. Freshwater Biol. 23: 181–189.

CUDNEY, M. D. ET J. B. WALLACE. 1980. Life cycles, microdistribution and production dynamics of six species of net-spinning caddisflies in a large southeastern (U.S.A.) river. Holart. Ecol. 3: 169–182.

FREEMAN, M. C. ET. J. B. WALLACE. 1984. production of net-spinning caddisflies (Hydropsychidae) and black flies (Simuliidae) on rock outcrop substrate in a small Piedmont stream. Hydrobiologia 112: 3–15.

GIBERSON, D. J. ET T. D. GALLOWAY. 1985. Life history and production of *Ephoron album* (Say) (Ephemeroptera: Polymitarcidae) in the Valley River, Manitoba. Can. J. Zool. 63: 1668–1674.

GRZYBKOWSKA, M. ET J. WITCZAK. 1990. Distribution and production of Chironomidae (Diptera) in the lower course of the Grabia River. Freshwater Biol. 24: 519–531.

HAMILL, S. E. 1975. Production of sphaeriid clams and amphipods crustaceans in the Ottawa River near Ottawa–Hull, Canada. Thèse de maîtrise, Université d'Ottawa, Ottawa (Ontario). 98 p.

HAMILL, S. E., S. U. QUADRI ET G. L. MACKIE. 1979. Production and turnover ratio of *Pisidium casertanum* (Pelecypoda: Sphaeriidae) in the Ottawa River near Ottawa–Hull, Canada. Hydrobiologia 62: 225–230.

HUMPHREYS, W. F. 1981. Towards a simple index based on live-weight and biomass to predict assimilation in animal populations. J. Anim. Ecol. 50: 543–561.

HURYN, A. D. ET J. B. WALLACE. 1985. Life history and production of *Goerita semata* Ross (Trichoptera: Limnephilidae) in the southern Appalachian Mountains. Can. J. Zool. 63: 2604–2611.

1987a. Production and litter processing by crayfish in an Appalachian mountain stream. Freshwater Biol. 18: 277–286.

1987b. The exopterygote insect community of a mountain stream in North Carolina, USA: life histories, production, and functional structure. Aquat. Insects 9: 229–251.

1988. Community structure of Trichoptera in a mountain stream: spatial patterns of production and functional organization. Freshwater Biol. 20: 141–155.

IVERSEN, T. M. 1980. Densities and energetics of two streamliving larval populations of *Sericostoma personatum* (Trichoptera). Holarct. Ecol. 3: 65–73.

IVERSEN, T. M. ET J. JESSEN. 1977. Life-cycle, drift and production of *Gammarus pulex* L. (Amphipoda) in a Danish spring. Freshwater Biol. 7: 287–296.

JACKSON, J. K. ET S. G. FISHER. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. Ecology 67: 629–638.

LAUZON, M. ET P. P. HARPER. 1986. Life history and production of the stream–dwelling mayfly *Habrophlebia vibrans* Needham (Ephemeroptera: Leptophlebiidae). Can. J. Zool. 64: 2038–2045.

LAZIM, M. N. ET M. A. LEARNER. 1986. The life-cycle and productivity of *Tubifex tubifex* (Oligochaeta; Tubificidae) in the Moat-Feeder stream, Cardiff, South Wales. Holarct. Ecol. 9: 185–192.

MACKAY R. J. ET T. F. WATERS. 1986. Effects of small impoundments on hydropsychid caddisfly production in Valley Creek, Minnesota. Ecology 67: 1680–1686.

MANN, K. H. 1969. The dynamics of aquatic ecosystems. Adv. Ecol. Res. 6: 1–81.

MORIN, A., T. A. MOUSSEAU ET D. A. ROFF. 1987. Accuracy and precision of secondary production estimates. Limnol. Oceanogr. 32: 1342–1352.

MORIN, A., C. BACK, A. CHALIFOUR, J. BOISVERT ET R. H. PETERS. 1988a. Empirical models predicting ingestion rates of black fly larvae. Can. J. Fish. Aquat. Sci. 45: 1711–1719.

MORIN, A., M. CONSTANTIN ET R. H. PETERS. 1988b. Allometric models of simuliid growth rates, and their use for estimation of production. Can. J. Fish. Aquat. Sci. 45: 315–324.

MURPHY, P. M. ET M. A. LEARNER. 1982. The life history and production of *Asellus aquaticus* (Crustacea: Isopoda) in the River Ely, South Wales. Freshwater Biol. 12: 435–444.

PARKER, C. R. ET J R. VOSHELL JR. 1983. Production of filter-feeding Trichoptera in an impounded and a free-flowing river. Can. J. Zool. 61: 70–87.

PETERS, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.

PLANTE, C. ET J. A. DOWNING. 1989. Production of freshwater invertebrate populations in lakes. Can. J. Fish. Aquat. Sci. 46: 1489–1498.

1990. Empirical evidence for differences among methods for calculating secondary production. J. N. Am. Benthol. Soc. 9: 9–16.

RICHARDSON, T. D., J. F. SCHEIRING ET K. M. BROWN. 1988. Secondary production of two lotic snails (Pleuroceridae: *Elimia*). J. N. Am. Benthol. Soc. 7: 234–245.

RIGLER, F. H. ET J. A. DOWNING. 1984. The calculation of secondary productivity, p. 19–59. *Dans* J. A. Downing et F. H. Rigler [ed.] A manual of methods for the assessment of secondary productivity in fresh waters. International Biological Programme Handbook No. 17. 2nd ed. Blackwell Scientific Publications, Oxford.

ROEDING, C. E. ET L. A. SMOCK. 1989. Ecology of macroinvertebrate shredders in a low-gradient sandy-bottomed stream. J. N. Am. Benthol. Soc. 8: 149–161.

ROSILLON, D. 1986. Life cycle, growth, mortality and production of *Ephemerella major* Klapalek (Ephemeroptera) in a trout stream in Belgium. Freshwater Biol. 16: 269–277.

ROSS, D. H. ET J. B. WALLACE. 1983. Longitudinal patterns of production, food consumption, and seston utilization by net-spinning caddisflies (Trichoptera) in a southern Appalachian stream (USA). Holarct. Ecol. 6: 270–284.

SHORT, R. A., E. H. STANLEY, J. W. HARRISON ET C. R. EPPERSON. 1987. Production of *Corydalus cornutus* (Megaloptera) in four streams differing in size, flow, and temperature. J. N. Am. Benthol. Soc. 6: 105–114.

SMOCK, L. A., E. GILINSKY ET D. L. STONEBURNER. 1985. Macroinvertebrate production in a southeastern United States blackwater stream. Ecology 66: 1491–1503.

WATERS, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 10: 91–164.

WATERS, T. F. ET J. C. HOKENSTROM. 1980. Annual production and drift of the stream amphipod *Gammarus pseudolimnaeus* in Valley Creek, Minnesota. Limnol. Oceanogr. 25: 700–710.

Allochthonous versus Autochthonous Organic Matter Contributions to the Trophic Support of Fish Populations in Clear-Cut and Old-Growth Forested Streams

Robert E. Bilby and Peter A. Bisson

Weyerhaeuser Company, Technology Center, Tacoma, WA 98477, USA

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Can. J. Fish. Aquat. Sci. 49: 540–551.

Annual organic matter inputs and production of stocked coho salmon (*Oncorhynchus kisutch*), coastal cutthroat trout (*O. clarki clarki*), and shorthead sculpin (*Cottus confusus*) from spring through early autumn were monitored for 2 yr in two headwater tributaries of the Deschutes River, Washington. One site was bordered by old-growth coniferous forest; the other was an area clear-cut without buffer strips 7 yr before the study. Allochthonous organic matter (terrestrial origin) dominated inputs to the old-growth site and contributed ~300 $g \cdot m^{-2} \cdot yr^{-1}$, while autochthonous organic matter totaled ~100 $g \cdot m^{-2} \cdot yr^{-1}$. In the clear-cut site, autochthonous inputs contributed ~175 $g \cdot m^{-2} \cdot yr^{-1}$, but allochthonous inputs contributed only ~60 $g \cdot m^{-2} \cdot yr^{-1}$ owing to loss of riparian vegetation. Although combined allochthonous and autochthonous inputs were almost twofold greater in the old-growth site, fish production was greater in the clear-cut site. Production of coho salmon and shorthead sculpin during early summer was largely responsible for differences between sites. Fish populations appeared to depend upon food derived from autotrophic pathways during spring and summer in the presence or absence of forest canopy, a hypothesis supported by analysis of coho stomach contents and the similar ratios of autochthonous inputs and fish production between the two streams.

Pendant 2 ans, on a étudié l'apport de matière organique et la production annuels de saumon coho (*Oncorhynchus kisutch*) d'élevage, de truite fardée côtière (*O. clarki clarki*) et de chabot à tête courte (*Cottus confusus*) (et ce du printemps au début de l'automne) dans deux tributaires d'amont de la rivière Deschutes, dans l'État de Washington. Le premier site était ombragé par un peuplement mûr de conifères tandis que le second avait été coupé à blanc, sans création de zone tampons, sept ans avant la réalisation de la présente étude. Au premier site, la matière organique allochtone d'origine terrestre était la composante principale de l'apport, soit ~300 $g \cdot m^{-2} \cdot an^{-1}$, tandis que la matière organique autochtone totalisait ~100 $g \cdot m^{-2} \cdot an^{-1}$. Au deuxième site, l'apport autochtone s'élevait à ~175 $g \cdot m^{-2} \cdot an^{-1}$, mais l'apport allochtone n'atteignait que ~60 $g \cdot m^{-2} \cdot an^{-1}$ à cause de la perte de végétation ripicole. Même si les apports allochtone et autochtone combinés étaient presque deux fois plus élevés au premier site, la production de poisson était supérieure au deuxième site. La production de saumon coho et de chabot à tête courte au début de l'été expliquait en grande partie cette différence. Au printemps et à l'été, les populations de poisson semblaient dépendre d'aliments dérivés de réseaux autotrophes, un présence ou en l'absence d'un couvert forestier. Cette hypothèse est étayée par les résultats d'une analyse des contenus stomacaux de saumons cohos et les rapports semblables des apports autochtones et de la production de poisson entre les deux cours d'eau.

Received October 29, 1990
Accepted October 4, 1991
(JA776)

Reçu le 29 octobre 1990
Accepté le 4 octobre 1991

Organic matter budgets of small streams flowing through forested watersheds are dominated by inputs of terrestrial material (Fisher and Likens 1973; Naiman and Sedell 1979; Cummins et al. 1982; Triska et al. 1982). This dominance is caused by high input rates of material from allochthonous sources coupled with suppression of autochthonous production by heavy shading from terrestrial vegetation (Gregory 1980). Removal of riparian vegetation through timber harvest reverses the relative importance of allochthonous and autochthonous organic sources by stimulating primary production and decreasing inputs of terrestrial organic matter (Hansmann and Phinney 1973; Stockner and Shortreed 1976; Murphy et al. 1981; Gregory et al. 1987).

Greater autochthonous production and decreased inputs of terrestrial materials influence consumer trophic levels within the stream (Murphy and Meehan 1991). Invertebrates that consume autochthonous energy sources benefit from improved food resources when more sunlight reaches the stream channel, nutrient concentrations are elevated, and algal growth is stimulated (Weber 1981; Kirchofer 1984; Murphy 1984; Wallace and Gurtz 1986; Perrin et al. 1987). Overall, invertebrate production may increase after logging (Wallace and Gurtz 1986; Behmer and Hawkins 1986), due in part to the generally higher protein content and digestability of algae and algal-based detritus than most incoming terrestrial plant material (Triska et al. 1975) and to a change in community composition from predominantly univoltine detritivores to multivoltine grazers and collector-gatherers (Gregory et al. 1987).

Increased density, biomass, and production of salmonids in streams flowing through clear-cut areas have also been documented (Murphy and Hall 1981; Hawkins et al. 1983; Bisson and Sedell 1984), but enhancement of food resources after for-

TABLE 1. Characteristics of the two study sites during summer low-flow conditions. Pool and riffle classification from Bisson et al. (1982).

	Clear-cut site	Old-growth site
Section length (m)	377	451
Wetted surface area (m^2)	872	1502
Stream order	4th	4th
Watershed area (ha)	255	850
Pools (% of total area)		
Backwater	5.6	6.0
Scour	16.1	25.7
Plunge	8.7	23.9
Secondary channel	2.0	2.1
Dammed	0	1.1
Total	32.4	58.8
Riffles (% of total area)		
Low-gradient riffles	23.3	14.7
Rapid	3.3	8.1
Cascades	41.0	18.4
Total	67.6	41.2

est canopy removal may in some cases be masked by degradation of other aspects of the stream environment (Everest et al. 1987; Bisson et al. 1987; Scrivener and Brownlee 1989). Other factors potentially contributing to increased salmonid production in open areas include elevated water temperatures resulting in earlier emergence and a prolonged spring growing period (Hartman et al. 1987; Holtby 1988) and enhanced feeding efficiency (Wilzbach 1985).

Changes in the types and quantities of organic matter entering stream food webs following logging may also contribute to changes in fish production. Our objective was to compare differences in organic matter sources, amounts, and seasonal timing of inputs over 2 yr in a stream segment flowing through an old-growth forested watershed with a segment in an adjacent stream flowing through a clear-cut area. Production dynamics of fishes in each system were examined relative to differences in the form and amount of available energy resources. The principal question was: ‘‘Would increased production of autochthonous organic matter after logging offset losses of allochthonous material in the trophic support of fish populations?’’

Materials and Methods

Watershed and Study Site Description

The two study streams, Upper Deschutes River and West Fork Creek, are located in the headwaters of the Deschutes River drainage system in western Washington State (46°43′N, 122°23′W). Both are underlain by andesitic bedrock of the Northcroft Formation (Schasse 1987). Most of the 255-ha Upper Deschutes River watershed was clear-cut logged in 1974–75 and replanted with Douglas-fir (*Pseudotsuga menziesii*) and noble fir (*Abies procera*) in 1975–76. At the time of the study the riparian zone of this stream consisted of young willow (*Salix* spp.), red alder (*Alnus rubra*), conifers, and dense growths of shrub and herbaceous vegetation. The adjacent 850-ha West Ford Creek watershed was undisturbed at the time of the study and was dominated by Douglas-fir, western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). Although the sites differed in drainage area (Table 1), streamflow differences between the two watersheds were smaller than would be expected due to greater precipitation at the clear-cut site (Bilby and Bisson 1987). Mean annual discharge at the old-growth site was 1.12 $m^3 \cdot s^{-1}$ in 1982 and 1.11 $m^3 \cdot s^{-1}$ in 1983. Corresponding discharge values at the clear-cut site were about half of those at the old-growth watershed, being 0.65 and 0.64 $m^3 \cdot s^{-1}$ for 1982 and 1983, respectively.

Stream segments chosen for study (Table 1) were bounded by natural barriers to upstream fish passage at their upstream ends and by a fish trap at their downstream ends. The old-growth segment was longer and had a greater surface area than the clear-cut site. Abundance of large woody debris was low at the clear-cut site because the channel had been cleaned after logging; as a consequence, pools were less abundant at the clear-cut site than at the old-growth site.

Allochthonous Inputs

Inputs of allochthonous organic matter were sampled with six litter traps suspended over the streams at randomly selected locations. The traps had 1-mm-mesh bottoms and were positioned 1.5 m above the water surface to avoid damage during high discharge. In addition, six litter traps were placed adjacent to each stream with trap openings facing upslope to sample organic matter entering the channel from the forest floor. Traps were emptied monthly from June 1982 through May 1984.

Inputs from herbaceous vegetation growing within the channel margins or overhanging the streams less than 1.5 m above the water surface were estimated from plots. Rooted vascular plants within the high-flow channel margins were collected to a height of 1.5 m at 10 randomly selected 1-m^2 plots. We assumed that all plant material growing within high-flow margins would become part of the organic matter inputs at some time each year. Vegetation overhanging the channel less than 1.5 m above the water surface was sampled by selecting 10 1-m-long sections of the high-flow bank at each site and collecting all nonwoody material above ground level to a height of 1.5 m from the water line, again assuming that all organic matter would be delivered to the stream each year.

Samples from litter traps and vegetation plots were oven dried at 60°C and separated into five categories: wood, moss and lichens, needles, leaves, and flowers and fruit. Material in each category was then redried and weighed. Following weighing, subsamples were combusted at 500°C and organic matter was determined by weight loss on ignition.

Inputs of dissolved organic carbon (DOC) from groundwater to the two study sections were not estimated during the study. Due to the relatively short length of the sites, addition of organic matter by this pathway was assumed to be small. Hyporheic storage and recycling of DOC was also not measured within the study reaches. Although this has been shown to be an important fate of soluble nutrients within some small forested streams (Triska et al. 1989), our organic matter budget did not consider differences in groundwater storage between the two sites.

Autochthonous Inputs

Autochthonous production was measured in situ with light and dark photosynthesis–respiration chambers (Bott et al. 1978). Flow in the 66 × 31 × 8 cm chambers was regulated by two submersible pumps that were run continuously throughout incubation periods. Trays filled with gravel and left undisturbed in the stream for a minimum of 3 wk were placed in the chambers and incubated 0.5–2.0 h, depending upon the rate of oxygen production. Dissolved oxygen was measured with an oxygen–temperature probe fitted into the wall of the chambers. All incubations took place between 10:30 and 14:00 PST. Light intensity during an incubation period was recorded every 0.5 h with a dome solarimeter. A photosynthetic quotient of 1.2 was used to convert change of oxygen concentration to amount of fixed carbon (Wetzel and Likens 1979). The total amount of fixed organic matter was estimated by dividing the carbon values by 0.47 (Vollenweider 1974). Measurements in each stream were taken at about 10-d intervals during spring and summer months. Photosynthesis during autumn and winter was measured less frequently.

Solar input to the streams was extrapolated from light measurements taken near Olympia, Washington, at the mouth of the Deschutes River (Cinquemani et al., U.S. National Oceanic and Atmospheric Administration undated report). Measurements from Olympia, 50 km from the study area, were applied directly to the clear-cut site. However, the forest canopy over the old-growth site reduced incoming solar radiation, necessitating a correction. Decreased light inputs to the old-growth stream were estimated by comparing light intensity measurements taken simultaneously with a dome solarimeter at the old-growth site and the clear-cut site under different cloud cover conditions.

Primary production was estimated from regressions of gross photosynthesis against light intensity, a procedure used for other small forested streams by Murphy (1984). Regressions were developed for each site during each of three intervals: July–October, November–February, and March–June. These time intervals corresponded to periods of similar water temperature and discharge regimes. During the July–October period, water temperatures were relatively warm and streamflow was low and stable. From November to February, water temperatures were low and streamflows tended to be high and extremely variable; nearly all major freshets occurred at this time of year. Water temperature and streamflows from March to June were intermediate relative to the two other periods.

Fluvial Inputs

Organic matter contributed to the study reached by fluvial transport was separated into three categories based on particle size. Dissolved organic matter (DOM) was material <0.001 mm diameter and was measured as DOC, fine particulate organic matter (FPOM) ranged from 0.001 to 1.0 mm, and coarse particulate organic matter (CPOM) was material >1.0 mm. Fluvial transport samples were collected during 1984, with the exception of two months when the sites were not accessible. Grab samples were analyzed for DOC with an infrared gas analyzer after digesting an aliquot of filtered water with $K_2S_2O_8$ (Menzel and Vaccaro 1964).

FPOM concentration was measured in water samples drawn with automatic pump samplers (1-mm-mesh intakes) and chosen to represent concentration changes over the full range of flow conditions during the study period. FPOM samples were filtered through precombusted and preweighed glass fiber filters and dried at 60°C. After reweighing to determine the total weight of particulate material, filters were ashed at 500°C and organic matter content was determined by weight loss on ignition.

CPOM was sampled by placing 1-mm-mesh drift nets in the streams at a wide range of flows. During periods of low discharge, nets sampled the entire flow of the stream for up to 24 h. Volume of water passing through the net was equivalent to discharge when the entire streamflow was being sampled. During freshets, a 55-cm-wide net was placed in the channel from 1 to 30 min. Volume of water sampled was determined by measuring flow through the net at the start and end of a collection period using a current velocity meter. CPOM samples were dried, separated into the five categories used for litter samples, weighed, and then the litter categories were recombined. A subsample was drawn from each sample for determination of organic content through weight loss on ignition.

Fisher (1977) and Cummins et al. (1982) have discussed difficulties in comparing fluvial inputs of particulate organic matter with inputs from other sources in stream reaches of unequal length. Because the lengths of our study sites were not equal, the relative importance of material transported into the sites from upstream sources varied. Input from terrestrial vegetation or from primary production was dependent upon the surface area of the sites whereas fluvial inputs were dependent only upon organic matter concentration and stream discharge and were not significantly influenced by the area of the sites. However, relative differences in the availability of fluvially transported material to the stream's biota were indexed by computing mean monthly organic matter concentrations, weighted for flow, at each site. Relationships between CPOM and FPOM concentration and discharge were developed over a wide range of flow conditions at each study site. The mean monthly concentration of particulate organic matter transported to the sites was calculated from average daily values based on the relationship between concentration and discharge and weighted by mean daily flow.

We also monitored discharge, stream temperature, and nutrient concentrations. Daily streamflow at the sites was estimated by correlating readings on rated staff gauges with simultaneous readings on a nearby stream with a similar flow patterns and equipped with a gauge height recorder. Electronic thermographs recorded daily maximum, minimum, and mean water temperatures. Grab samples of nutrients (nitrate-N, ammonia-N, Kjeldahl-N, and total P) were collected monthly and analyzed by standard methods (American Public Health Association et al. 1975).

Fish Populations

Two species resided naturally in the streams, coastal cutthroat trout (*Oncorhynchus clarki clarki*) and shorthead sculpin (*Cottus confusus*). Cutthroat trout were found by Bisson and Sedell (1984) to be more abundant in the Upper Deschutes River than in West Ford Creek during the late 1970s. Bilby and Bisson (1987) also reported that cutthroat trout and shorthead sculpin densities and biomasses were significantly greater in the clear-cut than in the old-growth site during the 3 yr prior to this study.

Juvenile coho salmon (*Oncorhynchus kisutch*) of hatchery origin (South Puget Sound stock from the Washington Department of Fisheries Puyallup River hatchery) were released at each site on June 15, 1982, and May 5, 1983. The number of fish was adjusted for differences in site area so that identical initial densities (number per square metre) were planted into the streams (Bilby and Bisson 1987). However, the total number, time of stocking, and size of coho fry changed from 1982 to 1983. Difference in stocking time and size at stocking was determined by availability of fry at the hatchery. Stocking densities of coho in 1982 were approximately 16 fry·m^{-2}, while stocking densities in 1983 were approximately 9 fry·m^{-2}. Subsamples of planted fry indicated that there was no difference in initial size or condition factor between the sites in either year (*t*-test, $p < 0.01$). Average weight of coho fry at release was 1.88 g in 1982; in 1983, fish averaged 0.75 g.

Our purpose in stocking was to evaluate the response of juvenile coho to differences in organic matter sources independent of differences in recruitment rates between the two streams. Changes in stocking density from 1982 to 1983 permitted examination of compensatory effects of population pressure on survival and growth. Although we could not control the abundance of resident trout and sculpins at the outset, the ability to stock coho above a natural barrier (Deschutes Falls) facilitated a comparison of production rates in streams where initial populations were under strict experimental control. In doing so, we were forced to assume that hatchery coho fry would respond in the same manner to conditions in the streams as would naturally produced fry, an untested assumption.

Fish populations were censused in early summer and early autumn. Efforts to obtain midwinter population estimates failed owing to high streamflow and inability to assess the sites. Therefore, our results extended over only part of the annual cycle, albeit the period when most growth occurred. We found (Bilby and Bisson 1987) that the majority of juvenile coho rearing in the sites in early autumn emigrated from the streams with the onset of winter conditions (high discharge and low temperatures), a pattern consistent with observations elsewhere in the Pacific Northwest of coho salmon moving from headwater streams to favorable winter habitat lower in the drainage system (Peterson 1982; Brown and Hartman 1988). A survey of the winter distribution of coho salmon in the Deschutes River in 1984 (P. A. Bisson, unpubl. data) located large numbers of fish downstream in small, spring-fed tributaries and sloughs along the flood plain. Although it would have been preferable to describe the production of coho salmon in our headwater study sites throughout the year, we feel that spring and summer measurements accurately reflected most of the relative contribution of allochthonous and autochthonous organic matter to this species while rearing in headwater streams.

Randomly selected pools and riffles (habitat units) within the streams were electrofished three times and the number of fish present in each habitat unit was estimated using the removal summation technique of Carle and Strub (1978). Fork lengths were measured to the nearest millimetre, and all fish were returned to the channel unit from which they had been collected. Total numbers of fish in the entire reach were estimated by multiplying the average density for a given type of habitat by the total surface area of that habitat type present in the study section (Bilby and Bisson 1987). Biomass estimates were based on length–weight regressions established from 30 fish selected randomly from each site on each sample date. When fewer than 30 individuals of a species were available for length–weight determinations, all fish were used.

Downstream movements were monitored with fish traps at the lower end of each study site. Actual mortality was calculated as the difference between the estimated population size and the number of downstream migrants. Production estimates (Chapman 1978) assumed that instantaneous daily rates of growth and ''mortality'' (actual mortality plus emigration) were exponential.

Stomach contents were sampled by flushing during June and July 1982 to determine differences in types of food organisms selected by coho salmon in the two sites. Thirty coho fry were selected at random from each stream for food analysis. Stomach samples from all fish were combined prior to sorting and identification. Classification of stomach contents included only items that were mostly intact; invertebrate fragments, exuviae, and unidentifiable items were not counted. Invertebrates in stomach samples were assigned to functional groups according to Merritt and Cummins (1978).

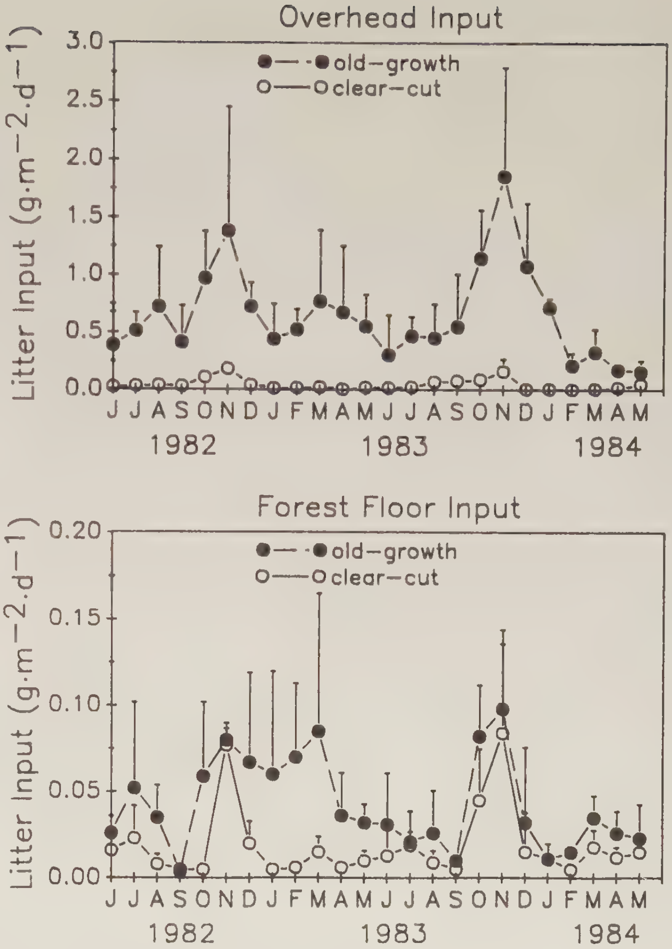


FIG. 1. Monthly input of terrestrial litter (mean ± 1SD) to the study sites from June 1982 through May 1984.

Differences in taxonomic composition and functional groups in the invertebrate drift of both streams were also examined. Six 24-h drift samples were taken from August 19 through August 22, 1984. Several rectangular drift nets of 202-μm mesh were placed together in riffles so as to sample as much of the streamflow as possible. Nets were emptied every 2 h over the 24-h sample period.

Fish stomachs and invertebrate drift were sampled only once during the study, and then not simultaneously. We therefore considered them only a crude approximation of the proportions of different invertebrate functional groups available to coho salmon in the two streams. Because samples were limited, comparison of the actual abundance of invertebrates at the sites was not attempted. Nevertheless, the proportion of various groups in the diet enabled us to draw some inferences about the relative contribution of different organic matter sources to the trophic support of coho salmon populations.

Results

Allochthonous Inputs

The amount of terrestrial litter collected in the suspended traps was significantly greater (*t*-test, $p < 0.05$) at the old-

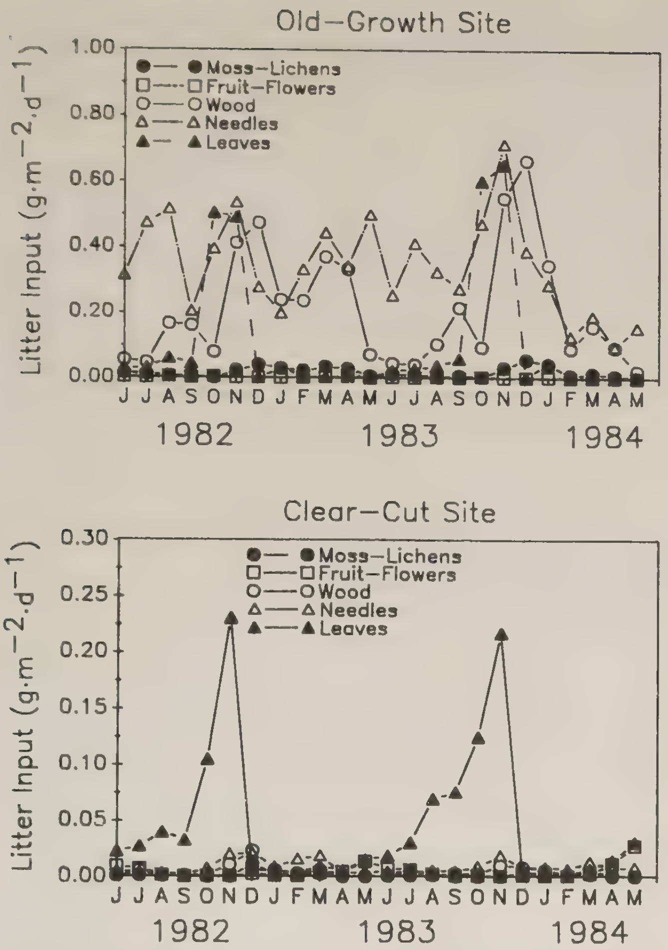


FIG. 2. Composition of terrestrial litter entering the study sites from June 1982 through May 1984.

TABLE 2. Summary of organic matter inputs to the two study sites from allochthonous and autochthonous sources.

	Organic inputs ($g \cdot m^{-2} \cdot yr^{-1}$)			
	Clear-cut site		Old-growth site	
Source	1982–83	1983–84	1982–83	1983–84
Allochthonous inputs				
Litterfall	16.9	16.2	245.9	222.7
Forest floor	6.0	7.7	18.4	12.5
In-stream vegetation[a]	36.3	36.3	60.7	60.7
Total	59.2	60.2	325.0	295.9
Autochthonous inputs				
Primary production	185.3	166.9	111.1	108.8
Total inputs	244.5	227.1	436.1	404.7

[a] Input values for herbaceous vegetation growing in the channel and overhanging vegetation less than 1.5 m above the water surface were determined for 1983–84 only. This value was used for both years of the study.

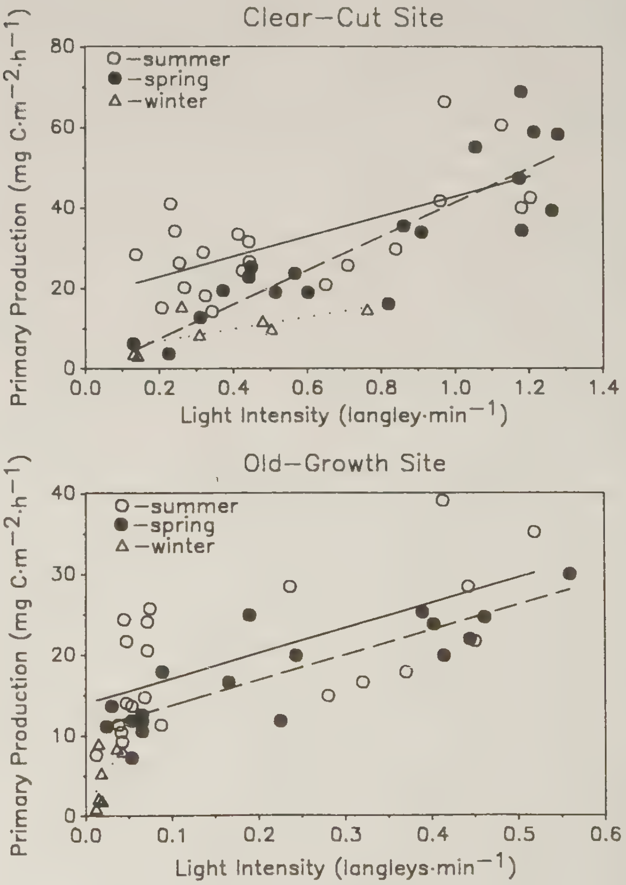


FIG. 3. Relationship between rate of gross primary production (GPP) and light intensity (LI) for the two study streams. Clear-cut site: spring, GPP = 42.38(LI) − 0.89 (r^2 = 0.77); summer, GPP = 24.96(LI) + 18.02 (r^2 = 0.44); winter, GPP = 14.83(LI) + 4.02 (r^2 = 0.48). Old-growth site: spring, GPP = 31.09(LI) + 10.69 (r^2 = 0.74); summer, GPP = 31.25(LI) + 14.00 (r^2 = 0.40); winter, GPP = 176.26(LI) + 1.09 (r^2 = 0.37).

growth site than at the clear-cut site at all times (Fig. 1). The greatest amounts of litter entered the streams in autumn. However, relatively large quantities entered the old-growth site throughout the year, while nearly all litter input to the clear-cut from overhead vegetation occurred over a short period.

Inputs of organic matter blowing into the streams along the forest floor were also significantly greater ($p < 0.05$) at the old-growth site than at the clear-cut site, but differences between the two streams were less for this material than for litter from the vegetative canopy (Fig. 1). There was a clear seasonal trend in the delivery of forest floor litter to the stream in the clear-cut watershed, with a peak in November of both years. Litter entering the old-growth site from the forest floor also tended to be greater in the autumn, but seasonal input differences were less distinct.

Leaves were the most common type of material collected in litter traps at the clear-cut site (Fig. 2), where most litter entered the stream in autumn. All other categories of terrestrial litter made only minor contributions to the clear-cut stream. The pattern of litter input essentially was dominated by autumn leaf fall from deciduous trees and herbaceous plants. A more constant input of allochthonous material to the old-growth site resulted from the greater diversity of litter sources and from temporal separation of peak periods of different types of litter production (Fig. 2). Leaves and needles were important components of autumn litter in the old-growth site, but this material was delivered to the stream throughout the year and was the most abundant type of litter in spring and summer. During winter, small pieces of wood were the most common type of litter input in the old-growth system.

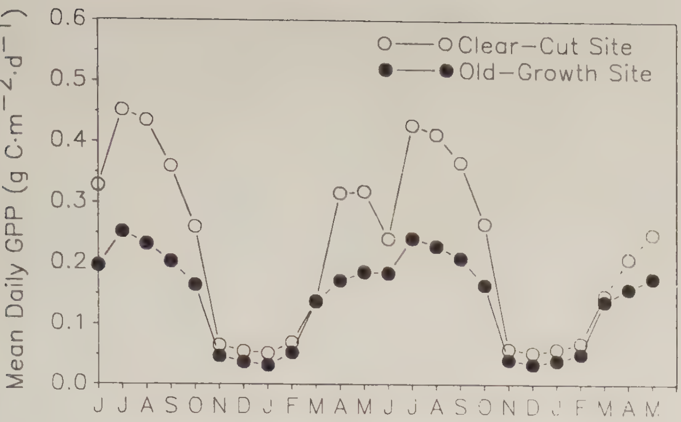


FIG. 4. Average daily primary production (GPP), by month, at the two study sites from June 1982 through May 1983.

Vegetation growing within or overhanging the channel less than 1.5 m above the water surface was an important source of the terrestrial organic matter at the clear-cut site (Table 2), where the proportion (60%) of allochthonous inputs contributed by in-channel and overhanging vegetation was nearly twice the amount from other sources. While the amount of this type of organic matter entering the stream was actually greater at the old-growth site, input from in-channel and overhanging vegetation was relatively less important (20%) due to the greater amounts of litter from other sources. Substantially more material was delivered to the old-growth stream by this pathway, however, than was delivered by transport across the forest floor.

Autochthonous Inputs

The relationships between gross primary production and light intensity at the clear-cut site differed significantly among spring, summer, and winter (Fig. 3, analysis of covariance, $p < 0.001$). Seasonal variations in water temperature, discharge, and a shift from green algae in spring to diatoms in summer were likely responsible for this difference. The relationships between gross primary production and light intensity were also significantly different among seasons at the old-growth site (Fig. 3, $p < 0.05$), but seasonal differences were somewhat less apparent than at the clear-cut site. The algal community in the old-growth stream was always dominated by diatoms. Total organic matter fixed by primary producers was calculated using estimated solar inputs (from climatological data) and the seasonal regressions between gross primary production and light intensity (Fig. 3).

At both sites, the amount of organic matter produced by autotrophic production was lowest during winter when there was relatively little difference in photosynthetic activity between the streams (Fig. 4). Highest levels of primary production occurred during summer, when the greatest differences between the old-growth and clear-cut sites were noted. Gross primary production was approximately twofold greater in the clear-cut than in the old-growth stream from April to October. Production of autochthonous organic matter was also relatively high during spring but dropped rather quickly in autumn. Rates of photosynthesis were similar for the two sites from November through March.

In spring, a dense growth of green algae, dominated by *Ulothrix* sp. and *Prasiola* sp., developed at the clear-cut site.

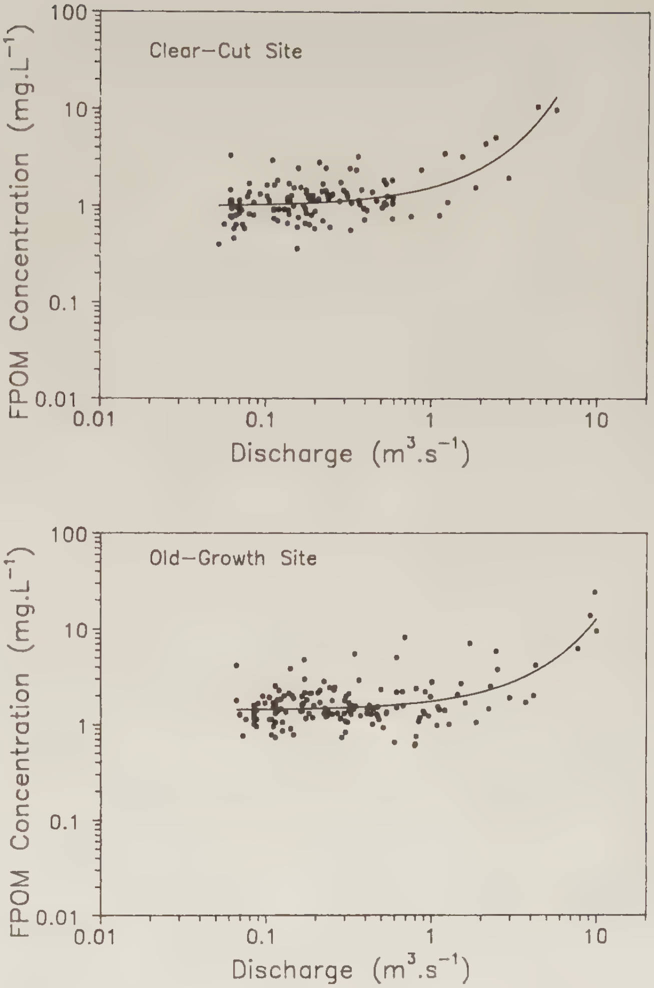


FIG. 5. Relationship between the concentration of fine particulate organic matter (FPOM) and discharge (Q) at the study sites. Clear-cut site: $\log_{10}(\mathrm{FPOM}) = 0.203(Q) - 0.004$ ($r^2 = 0.63$); old-growth site: $\log_{10}(\mathrm{FPOM}) = 0.096(Q) + 0.052$ ($r^2 = 0.61$).

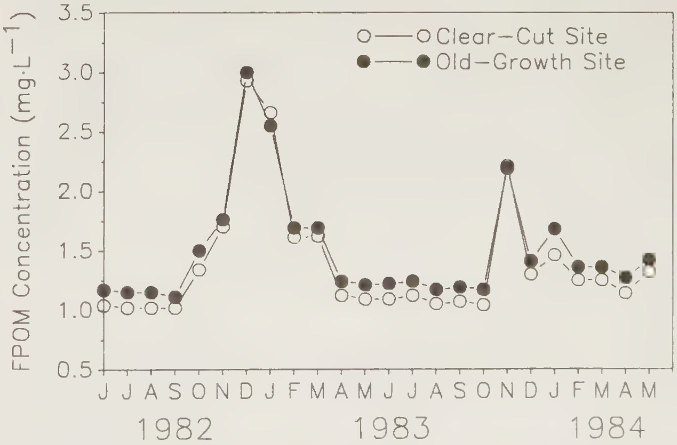


FIG. 6. Mean monthly fine particulate organic matter (FPOM) concentrations, weighted for discharge.

The green algae disappeared by early June, and diatoms dominated the algal community throughout summer and winter. Relatively little green algae was observed in spring at the old-growth site, where diatoms remained the dominant component of the algal community throughout the year.

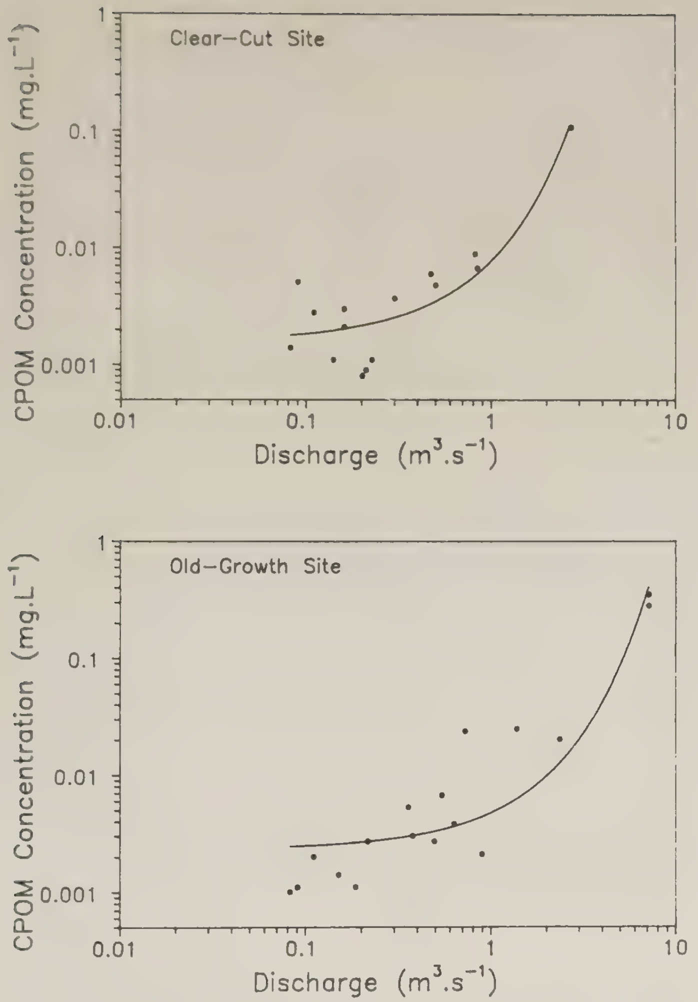


FIG. 7. Relationship between concentration of coarse particulate organic matter (CPOM) and discharge (Q) for the study sites. Clear-cut site: $\log_{10}(\mathrm{CPOM}) = 0.69(Q) - 2.80$ ($r^2 = 0.85$); old-growth site: $\log_{10}(\mathrm{CPOM}) = 0.31(Q) - 2.63$ ($r^2 = 0.82$).

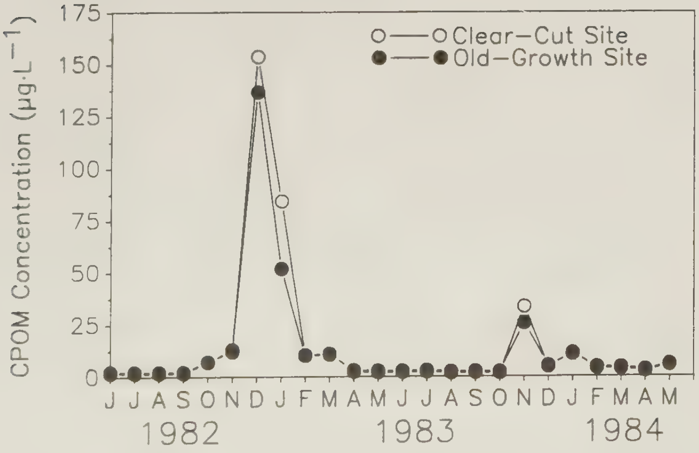


FIG. 8. Mean monthly coarse particulate organic matter (CPOM) concentrations, weighted for discharge.

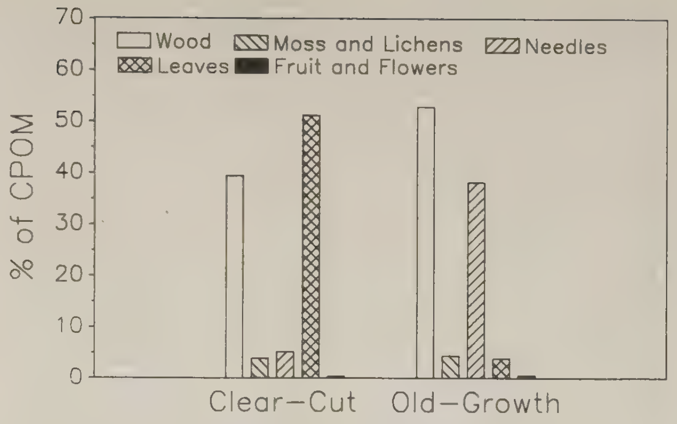


FIG. 9. Composition of coarse particulate organic matter (CPOM) collected at the two study sites.

TABLE 3. Concentrations of dissolved nutrients at the two study sites. *Significant differences between sites ($p < 0.05$) as determined by t-tests.

	Mean concentration ± 1 SE (µg·L^{-1})	
Nutrient species	Clear-cut site	Old-growth site
Kjeldahl-N	65 ± 18	59 ± 11
Ammonia-N	18 ± 5	20 ± 6
Nitrate + nitrite-N	9 ± 1*	22 ± 4*
Total dissolved P	19 ± 6	19 ± 5

Fluvial Inputs

Concentrations of DOC in the two streams were similar, averaging 1.31 and 1.21mg·L^{-1} at the clear-cut and old-growth sites, respectively. There was no seasonal pattern of DOC concentration changes nor any clear relationships between DOC concentration and discharge in either stream. Both streams possessed similar FPOM concentrations at low and moderate flows, with sharp increases occurring only at higher discharges (Fig. 5). As a result, monthly average FPOM concentrations (Fig. 6) were similar at the two sites.

CPOM increased slightly with discharge at low and moderate flows but exhibited a dramatic increase during high flows (Fig. 7). Concentrations of CPOM were much lower than those of FPOM in both streams, with values never in excess of 1 mg·L^{-1} at either site. Average monthly CPOM concentrations, weighted for discharge (Fig. 8), were similar at the two sites.

Woody material was an important component of the CPOM in both streams, accounting for approximately 40 and 50%, respectively, of the total dry weight of CPOM at the clear-cut and old-growth sites (Fig. 9). Deciduous leaves comprised slightly more than half of the CPOM in the clear-cut site, but only 5% of the CPOM in the old-growth site. Conifer needles made up about 40% of the CPOM at the old-growth site, but only about 5% of the CPOM in the clear-cut site. Abundances of other categories of CPOM were approximately the same in both systems.

Concentrations of dissolved nutrients were low at both study sites (Table 3), and no obvious seasonal patterns were apparent from the grab samples. Average nitrate-N concentrations were significantly greater in the old-growth site than in the clear-cut site over the period of study (t-test, $p < 0.05$). Differences in average Kjeldahl-N, ammonia-N, and total dissolved P concentrations between the two streams were not significant. Average atomic ratios of available N:P were 3.7 for the old-growth site and 4.8 for the clear-cut site, thus indicating that N was the nutrient most likely to limit primary production in both streams (Stockner and Shortreed 1978).

TABLE 4. Fish population statistics for the clear-cut (CC) and old-growth (OG) sites for each sample interval. Values are means followed by standard errors in parentheses. Density and biomass are given as terminal values for each interval. Growth rate and production values are estimated averages over the entire interval. Underlined values indicate significant differences (*t*-test, $p < 0.05$).

	Coho salmon		Cutthroat trout		Shorthead sculpin		Total all species	
	CC	OG	CC	OG	CC	OG	CC	OG
July 1982								
Density (number·m^{-2})	6.1 (1.2)	4.9 (1.2)	0.2 (0.1)	0.1 (0.1)	1.1 (0.3)	0.3 (0.1)	7.4 (1.4)	5.3 (1.2)
Biomass (g·m^{-2})	12.6 (2.6)	9.2 (2.2)	3.7 (1.5)	1.9 (0.8)	5.2 (1.9)	1.0 (0.3)	21.5 (4.6)	12.0 (2.6)
Growth rate (%·d^{-1})	0.43 (0.16)	0.11 (0.06)	0.39 (0.11)	0.60 (0.15)	0.20 (0.13)	0.19 (0.15)		
Production (mg·m^{-2}·d^{-1})	87.8 (27.1)	19.7 (6.1)	12.5 (4.7)	10.3 (1.6)	7.6 (2.9)	1.9 (0.6)	127.2 (24.8)	31.9 (25.8)
September 1982								
Density (number·m^{-2})	1.9 (0.3)	1.8 (0.5)	0.09 (0.04)	0.11 (0.04)	0.9 (0.8)	0.2 (0.1)	2.9 (0.7)	2.1 (0.5)
Biomass (g·m^{-2})	5.1 (1.0)	3.7 (0.9)	1.8 (0.8)	2.6 (1.3)	3.4 (0.9)	0.9 (0.4)	10.3 (2.1)	7.3 (1.8)
Growth rate (%·d^{-1})	0.41 (0.05)	0.18 (0.04)	0.45 (0.15)	1.10 (0.27)	0.06 (0.10)	0.22 (0.09)		
Production (mg·m^{-2}·d^{-1})	36.1 (7.1)	11.4 (3.2)	12.3 (7.1)	25.0 (7.1)	2.4 (0.5)	2.1 (0.3)	50.8 (13.5)	38.5 (8.7)
June 1983								
Density (number·m^{-2})	1.2 (0.5)	1.2 (0.3)	0.09 (0.04)	0.15 (0.04)	0.5 (0.2)	0.4 (0.1)	1.8 (0.6)	1.7 (0.3)
Biomass (g·m^{-2})	1.6 (0.5)	1.4 (0.3)	1.3 (0.6)	2.1 (0.9)	2.4 (1.0)	1.0 (0.3)	5.3 (1.3)	4.6 (1.0)
Growth rate (%·d^{-1})	1.9 (0.14)	1.4 (0.12)	0.22 (0.08)	0.09 (0.3)	0.15 (0.13)	−0.54 (0.14)		
Production (mg·m^{-2}·d^{-1})	77.3 (19.6)	54.5 (6.7)	3.3 (1.7)	1.9 (3.8)	3.2 (3.1)	−5.7 (1.8)	83.8 (15.1)	50.7 (3.7)
October 1983								
Density (number·m^{-2})	0.7 (0.3)	0.8 (0.2)	0.2 (0.1)	0.2 (0.1)	0.3 (0.1)	0.3 (0.1)	1.1 (0.4)	1.2 (0.3)
Biomass (g·m^{-2})	2.3 (0.9)	2.2 (0.6)	1.3 (0.6)	2.4 (1.0)	1.5 (0.4)	1.3 (0.6)	5.2 (1.1)	5.9 (1.8)
Growth rate (%·d^{-1})	0.69 (0.10)	0.86 (0.08)	0.49 (0.08)	0.09 (0.10)	0.16 (0.07)	0.48 (0.30)		
Production (mg·m^{-2}·d^{-1})	13.4 (5.2)	15.1 (2.2)	6.4 (2.1)	2.1 (1.9)	3.1 (0.9)	5.5 (3.1)	22.9 (4.1)	22.7 (5.1)

TABLE 5. Composition of invertebrate functional groups in August 1984 drift samples and in June–July 1982 coho salmon stomach samples.

	% of total number			
	Clear-cut site		Old-growth site	
Group	Drift	Diet	Drift	Diet
Scrapers	29.0	21.1	72.0	26.0
Collector-gatherers	48.1	69.7	21.9	64.6
Shredders	2.4	1.7	1.3	5.1
Predators	20.6	7.3	4.8	4.4

Fish Production

Production of all fish species over the early summer measurement period (Table 4) was greater in the clear-cut site than the old-growth site in both years (*t*-test, $p < 0.05$). In 1982, the average daily rate of fish production during early summer in the clear-cut site was 4.0 times greater than in the old-growth site, while in 1983 fish production in the clear-cut site exceeded the old-growth site by a factor of 1.7. No significant differences in total fish production were observed between the sites from late summer to early autumn.

Production of coho salmon accounted for 30–97% of the total production in the old-growth site and for 59–92% of the total production in the clear-cut site (Table 4). Initial stocking levels of fry influenced coho production rate (Bilby and Bisson 1987). At high stocking densities in 1982, coho production was primarily supported by the relatively large average biomass throughout summer and early autumn. In 1983, the year of lower initial densities, coho production was supported by high growth rates. In 1982, production of coho was greater in the clear-cut site than in the old-growth site throughout the summer, but in 1983 there was no significant difference in coho production between the streams.

Early summer production of shorthead sculpins was greatest in the clear-cut site in both years (*t*-test, $p < 0.05$), but sculpin production was generally lowest of the three species due to low growth rates (Table 4). Sculpin biomasses were comparable with the two salmonid species, except in 1982 when large numbers of stocked coho fry resulted in high coho biomasses. However, average biomass of shorthead sculpins was significantly greater in the clear-cut site than in the old-growth site in both years (Table 4).

Cutthroat trout production was not significantly different between the clear-cut and old-growth streams during any sampling period. Trout production was lower at both sites in 1983 than in 1982.

Food Habits

Most of the diet of coho salmon during June and July 1982 was composed of invertebrates belonging to scraper or collector-gatherer groups (Table 5). Likewise, invertebrate drift at both sites in August 1984 was dominated by these two functional groups. Principal scraper organisms in both drift and stomach samples were mayflies (*Baetis* spp.). The most abundant collector-gatherers were chironomid larvae belonging to the Orthocladiinae. Both taxa rely heavily on algae or algal-derived detritus as a primary food source (Lamberti and Moore 1984). Invertebrate predators were relatively abundant in drift samples from the clear-cut site; however, the vast majority of predators were mites, which were small and were found only infrequently in stomach samples. Shredders, which feed primarily on allochthonous organic matter, were rare in both drift and stomach samples. Terrestrial insects did not appear to be important components of coho diets in either stream at this time.

Discussion

Sources and amounts of organic inputs to the clear-cut and old-growth sites were considerably different. Autochthonous production in the clear-cut stream reach was about 70% greater than at the old-growth forested stream during 1982–83 and approximately 50% greater during 1983–84. In contrast, allochthonous input to the old-growth site was approximately fivefold greater than to the clear-cut site (Table 2). Organic matter from autochthonous production at the old-growth site amounted to about 35% of the input from terrestrial vegetation. At the clear-cut site, autochthonous production contributed about three times the amount of organic matter that was delivered from the terrestrial system.

Input rates of various forms of organic matter varied seasonally. Autochthonous production peaked in spring and summer and was likely related to elevated water temperature, high light intensity, extended photoperiod, and relatively stable streamflow. Increased availability of dissolved nutrients has been shown to stimulate algal growth and salmonid production (Johnston et al. 1990), but dissolved N or P concentrations were not greater at the clear-cut site during spring and summer. However, increases in nutrient availability may not have been reflected in the samples if uptake by algae had kept concentrations at low levels (Shortreed and Stockner 1982). Moreover, increases in nitrate-N seen in streams after clear-cutting in the Pacific Northwest (Fredriksen et al. 1975; Brownlee et al. 1988) were not observed in our clear-cut site. In fact, nitrate-N concentrations were significantly below those in the old-growth site, similar to the observed declines in the Carnation Creek, B.C., watershed after logging (Hartman and Scrivener 1990). Reduced nitrate levels in the clear-cut site may have been related to increased uptake by algae (Fig. 4), or alternatively, to increased nitrate uptake by the dense stand of 6-yr-old conifers that had been replanted in the clear-cut watershed (Vitousek and Reiners 1975).

Litter inputs to both sites were greatest in the autumn, although inputs from a variety of vegetation types growing along the stream continued at a fairly high level throughout the year at the old-growth site. Leaves from young deciduous vegetation (willows and alders) next to the clear-cut stream were the predominant source of terrestrial organic matter, yielding a pronounced autumnal peak in litter input (Fig. 2). Fluvial inputs peaked during winter months, when the majority of annual FPOM and CPOM transport often took place during a few days of elevated discharge.

Wood fragments dominated the CPOM component of fluvial allochthonous inputs, comprising 39 and 53% of the CPOM transported by streamflow at the clear-cut and old-growth sites, respectively. In contrast, wood constituted 10% of the litter input from terrestrial vegetation at the clear-cut site and 31% of the terrestrial input at the old-growth site. Net enrichment of wood in CPOM was probably caused by two factors: the lower rate of wood decomposition relative to other types of terrestrial organic matter (Harmon et al. 1986) and lack of tree fall to the streams during the study period. Because there was no tree fall into either reach from 1982 to 1984, measured wood input rates were very low. However, entry of large woody debris tends to be highly episodic in small streams (Bisson et al. 1987), and the absence of significant input during these three years may have resulted in underestimates of actual input rates over longer time periods. Because trees, especially conifers, decompose slowly in streams, woody material can be broken down and exported over periods of decades or more (Harmon et al. 1986). Patterns of storage and transport of wood fragments in Pacific Northwest streams are likely characterized by brief periods of large net gains followed by extended periods of gradual net losses. It appeared that our study took place during one of the latter periods.

TABLE 6. Average daily inputs of organic matter from allochthonous and autochthonous sources, average daily production of fishes from spring to early autumn, and the ratios of these values at the two study sites.

	Clear-cut (CC) (mg·m^{-2}·d^{-1})	Old-growth (OG) (mg·m^{-2}·d^{-1})	Ratio (CC/OG)
Annual organic matter inputs			
Allochthonous sources	164	851	0.19
Autochthonous sources	482	301	1.60
Fish production			
Coho salmon	34	18	1.89
Cutthroat trout	8.2	7.4	1.10
Salmonid (both species)	42	25	1.68
Shorthead sculpin	4.5	2.5	1.82
Total (all species)	47	18	1.67

Very little leaf material was present in CPOM samples from the old-growth site relative to its abundance in litter traps, indicating that most leaves were retained within the stream reach. Lack of leaf transport through the old-growth stream was probably caused by relatively fast decomposition (Triska et al. 1975; Lamberti and Moore 1984) coupled with retention of leaves by abundant large woody debris (Bilby and Likens 1980). Transport through the clear-cut site was greater because more leaves entered the stream from young deciduous trees growing along the banks and because there was much less large woody debris in the channel to trap incoming leaves. Therefore, a greater fraction of leaves and other terrestrial organic matter was retained in the old-growth site and was available for processing by aquatic invertebrates.

Differences in coho salmon growth rates between 1982 and 1983 (Table 4) suggested that food availability played a major role in controlling production of juvenile coho in the two streams. Coho growth rates were much lower when fish were very abundant than when densities were low. Compensatory growth responses indicated that food availability may have limited coho production more in the old-growth site than in the clear-cut site, an observation similar to findings in other Pacific Northwest streams (Gregory et al. 1987; Hicks et al. 1991). Production in the old-growth reach during the second year exceeded production in the first year in spite of an almost threefold greater average density of coho in 1982. In contrast, increased growth of coho in the clear-cut site during the low-density year was not sufficient to lead to greater production than in the high-density year, suggesting that compensatory growth limitation occurred to a greater extent in the old-growth stream and that food was probably less abundant there than at the clear-cut site.

Our results supported the hypothesis that organic matter derived from autochthonous sources is very important to fish populations even in heavily forested headwater streams. Total fish production in early summer was consistently greater in the clear-cut than in the old-growth site (Table 4), despite approximately five times more terrestrial organic matter entering the stream in the old-growth forest (Table 2). If detrital pathways dependent upon the processing of allochthonous material had been primarily responsible for providing trophic support to the fish (Mundie 1974), greater production should have been recorded at the old-growth site. Further evidence that organic matter of autochthonous origin was primarily responsible for supporting fish populations was seen in similarities of the ratios of fish production and autochthonous input between the clear-cut and old-growth sites (Table 6).

Composition of the invertebrate drift and coho stomach contents, based on limited samples, also indicated that autotrophic pathways were important in trophic support. The majority of invertebrates collected in drift and stomach samples are known to feed on algae or algal-based detritus. Shredders, which rely on terrestrial organic matter, were poorly represented in both the drift and diet of juvenile coho, at least at the time of year when our samples were taken. We noted that about 90% of the invertebrates eaten by coho in *both* the clear-cut and old-growth sites (Table 5) were those supported primarily by autochthonous organic matter. This suggests that autotrophic food pathways are important during summer regardless of the condition of the the forest canopy or the amount of allochthonous material entering the streams. At other times of the year, however, terrestrial invertebrates may become a dominant part of the diet (Mundie 1969), thus increasing the relative importance of organic matter of allochthonous origin to fish that reside in headwater streams year-round.

While increased primary and secondary production contributed to increased fish production at the clear-cut site, other factors may have played a role. The clear-cut stream exhibited higher maximum and average daily temperatures than the old-growth stream throughout spring and summer (Bilby and Bisson 1987). Moderate elevations in water temperature have been associated with increased salmonid growth in a small Vancouver Island stream (Holtby 1988; Hartman and Scrivener 1990), although these increases may not necessarily lead to improved survival later in the life cycle (Holtby and Scrivener 1989). In this study, temperatures at the clear-cut site were well within thermal tolerance ranges for salmonids; daily maxima usually ranged from 14 to 16°C and the absolute maximum temperature over the entire study period was 19°C. Average summer temperatures in the clear-cut site generally fell within a range considered optimum for coho salmon growth efficiency (Averett 1969). It is therefore possible that water temperature elevation at the clear-cut site contributed to the increase in salmonid production, although this would not have been likely without a corresponding increase in food availability (Bisson and Davis 1976). In addition, higher light levels at the clear-cut site may have enhanced feeding efficiency by rendering food items more visible (Wilzbach 1985).

Differences in coho salmon emigration after stocking also influenced production, especially at higher stocking rates in 1982 (Bilby and Bisson 1987). Immediately after stocking, fewer coho emigrated from the old-growth site, which contained better physical habitat quality (more pools) than the clear-cut site. This led to higher initial population densities in the old-growth stream and created a situation in which large numbers of fish were competing for apparently scarce food resources. As a consequence, growth rates of coho in the old-growth site were low in the spring and early summer (Bilby and Bisson 1987). At the clear-cut site, lower initial population densities coupled with apparently elevated food availability led to increased early summer growth rates and higher levels of production than at the old-growth site.

While this study demonstrated the importance of organic matter derived from autochthonous processes to the trophic support of fishes in summer, our results do not indicate whether increased spring and summer fish production in the clear-cut site was followed by increased winter production. Mason (1976) found that juvenile coho survived and grew better in a small stream with summer food supplementation, but that summer gains were lost in the absence of suitable overwintering habitat. Murphy and Meehan (1991) also noted that gains in summer production of salmonids may be lost if overwintering habitat is absent. Relatively few coho remained in either of our study streams at the beginning of the period of heavy winter storms, although more fish were present in the old-growth site at the end of summer than in the clear-cut site. Most coho emigrated from the streams in early autumn when streamflow increased and temperature declined. We estimated that only 0.5–8.1% of the initial number of resident fry, i.e. fish remaining in the streams after the initial pulse of downstream movement following stocking, were actually present in the sites by mid-October (Bilby and Bisson 1987). Thus, the results reflected the relative contributions of allochthonous and autochthonous organic matter sources to fish populations in the spring and summer rearing period, but not to fish production in the overwintering period.

Over the last decade, considerable effort has been expended in projects designed to enhance the rearing capacity of streams for juvenile salmonids. Almost without exception, enhancement procedures have involved manipulations of physical structure (logs or gabions) within the stream channel, or creation of off-channel overwintering areas. While both approaches can potentially increase the carrying capacity of the stream system for salmonids, we are not aware of any instance where habitat enhancement has been shown to increase primary and secondary production. Results of nutrient enrichment or food supplementation studies in streams in the Pacific Northwest have indicated that salmonid production can, under certain conditions, be significantly increased by trophic enhancement, sometimes dramatically (Warren et al. 1964; Mason 1976; Mundie et al. 1983; Johnston et al. 1990). Other workers have shown that both overwinter (Hartman et al. 1987; Hartman and Scrivener 1990) and ocean survival (Bilton et al. 1982; Peterman 1982; Wart and Slaney 1988) of anadromous salmonids improve with larger size. The benefits to be gained from increased freshwater growth and production might include higher smolt yield and, possibly, greater marine survival. However, Holtby and Scrivener (1989) showed that ocean survival was strongly influenced by complex interactions between smolt size, emigration timing, and winter and spring ocean conditions. Since our study did not include winter and ocean phases of the coho salmon life cycle, we are unable to conclude with certainty that increased production of autochthonous organic matter in headwater streams will lead to improved survival of coho salmon to adulthood.

Nevertheless, in view of the potential benefits of increased autotrophic production, we concur with Murphy and Meehan (1991) that management techniques designed to increase the supply of food to stream-dwelling salmonids warrant further investigation. If, as our study indicated, fish production in headwater streams is supported primarily by autochthonous organic matter sources, deliberate modification of nutrient concentrations (e.g. through fertilization) and incident light levels (e.g. through careful manipulation of vegetative canopy) may lead to significant increases in algal photosynthesis that are ultimately passed along to fish populations. The challenge is twofold: (1) to determine if autotrophic production can be increased to desired levels in a sustained, cost-effective, and practical manner and (2) to determine if such increases can be achieved without concurrent deterioration in the quality of other environmental components such as stream temperature or large woody debris, both on-site and downstream.

Acknowledgments

Funding for this study was provided by the Weyerhaeuser Company. We thank J. Heffner, J. Ward, J. Nielsen, B. Fransen, J. Witkowski, and D. Yoshida for technical assistance and M. Toland for statistical advice. S. V. Gregory, C. J. Perrin, and J. C. Scrivener provided much appreciated comments on an earlier version of the manuscript. The Washington Department of Fisheries donated coho salmon for the experiment and the Washington Department of Wildlife granted us permission to plant them in the two streams.

References

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, DC. 1193 p.

Averett, R. C. 1969. Influence of temperature on energy and material utilization by juvenile coho salmon. Ph.D. thesis, Oregon State University, Corvallis, OR. 75 p.

Behmer, D. J., and C. P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. Freshwater Biol. 16: 287–300.

Bilby, R. E., and P. A. Bisson. 1987. Emigration and production of hatchery coho salmon (*Oncorhynchus kisutch*) stocked in streams draining an old-growth and a clear-cut watershed. Can. J. Fish. and Aquat. Sci. 44: 1397–1407.

Bilby, R. E., and G. E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61: 1107–1113.

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426–447.

Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, K. V. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future, p. 143–190. *In* E. O. Salo and T. W. Cundy [ed.] Streamside management: forestry and fishery interactions. Institute of Forest Resources, Contribution 57, University of Washington AR-10, Seattle, WA. 471 p.

Bisson, P. A., and G. E. Davis. 1976. Production of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in a heated model stream. NOAA Fish. Bull. 74: 763–774.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow, p. 62–73. *In* N. B. Armantrout [ed.] Acquisition and utilization of aquatic habitat inventory information. Proceedings of a symposium held October 28–30, 1981, Portland, Oregon. The Hague Publishing, Billings, MT. 376 p.

Bisson. P. A., and J. R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington, p. 121–129. *In* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley [ed.] Fish and wildlife relationships in old-growth forests. American Institute of Fisheries Research Biologists, Juneau, AK. 425 p.

Bott, T. L., J. T. Brock, C. E. Cushing, S. V. Gregory, D. King, and R. C. Petersen. 1978. A comparison of methods for measuring primary productivity and community respiration in streams. Hydrobiologia 60: 3–12.

Brown, T. G., and G. F. Hartman. 1988. Contribution of seasonally flooded lands and minor tributaries to the production of coho salmon in Carnation Creek, British Columbia. Trans. Am. Fish. Soc. 117: 546–551.

Brownlee, M. J., B. G. Shepherd, and D. R. Bustard. 1988. Some effects of forest harvesting on water quality in the Slim Creek watershed in the central interior of British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1613: 41 p.

Carle, F. L., and M. R. Strub. 1978. A new method for estimating population size from removal data. Biometrics 34: 621–630.

Chapman, D. W. 1978. Production, p. 202–217. *In* T. Bagenal [ed.] Methods for assessment of fish production in fresh waters. Int. Biol. Prog. Handbook 3. Blackwell Scientific Publications, Oxford.

Cummins, K. W., J. R. Sedell, F. J. Swanson, G. W. Minshall, S. G. Fisher, C. E. Cushing, R. C. Petersen, and R. L. Vannote. 1982. Organic matter budgets for stream ecosystems: problems in their evaluation, p. 299–353. *In* G. W. Minshall and J. R. Barnes [ed.] Stream ecology: application and testing of general ecological theory. Plenum Press, New York, NY.

Everest, F. H., R. L. Beschta, J. C. Scrivener, K. V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production: a paradox, p. 98–142. *In* E. O. Salo and T. W. Cundy [ed.] Streamside management: forestry and fishery interactions. Institute of Forest Resources, Contribution 57, University of Washington AR-10, Seattle, WA. 471 p.

Fisher, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. Int. Rev. Gesamten Hydrobiol. Hydrogr. 62: 701–727.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421–439.

Fredriksen, R. L., D. G. Moore, and L. A. Norris. 1975. The impact of timber harvest, fertilization, and herbicide treatment on streamwater quality in western Oregon and Washington, p. 283–313. *In* B. Bernier and C. H. Winget [ed.] Forest soils and forest land management. Laval University Press, Quebec, Que. 675 p.

Gregory, S. V. 1980. Effects of light, nutrients, and grazing on periphyton communities in streams. Ph.D. thesis, Oregon State University, Corvallis, OR. 151 p.

Gregory, S. V., G. A. Lamberti, D. C. Erman, K. V. Koski, M. L. Murphy, and J. R. Sedell. 1987. Influence of forest practices on aquatic production, p. 233–255. *In* E. O. Salo and T. W. Cundy [ed.] Streamside management: forestry and fishery interactions. Institute of Forest Resources, Contribution 57, University of Washington AR-10, Seattle, WA. 471 p.

Hansmann, E. W., and H. K. Phinney. 1973. Effects of logging on periphyton in coastal streams of Oregon. Ecology 54: 194–199.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133–302.

Hartman, G. F., and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Can. Bull. Fish. Aquat. Sci. 223: 148 p.

Hartman, G. F., J. C. Scrivener, L. B. Holtby, and L. Powell. 1987. Some effects of different streamside treatments on physical conditions and fish population processes in Carnation Creek, a coastal rain forest stream in British Columbia, p. 330–372. *In* E. O. Salo and T. W. Cundy [ed.] Streamside management: forestry and fishery interactions. Institute of Forest Resources, Contribution 57, University of Washington AR-10, Seattle, WA. 471 p.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Can. J. Fish. Aquat. Sci. 40: 1173–1185.

Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Response of salmonid populations to habitat changes. Am. Fish. Soc. Spec. Publ. 19: 483–518.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 45: 502–515.

Holtby, L. B., and J. C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging and fishing on the numbers of chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) returning to Carnation Creek, British Columbia, p. 62–81. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105: 199 p.

Johnston, N. T., C. J. Perrin, P. A. Slaney, and B. R. Ward. 1990. Increased juvenile salmonid growth by whole-river fertilization. Can. J. Fish. Aquat. Sci. 47: 862–872.

Kirchofer, D. A. 1984. A stream ecosystem in an old-growth forest in southeast Alaska. Part 3: Standing crop and drift of invertebrates in Procupine Creek, p. 71–79. *In* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley [ed.] Fish and wildlife relationships in old-growth forests. American Institute of Fisheries Research Biologists, Juneau, AK. 425 p.

Lamberti, G. A., and J. W. Moore. 1984. Aquatic insects as primary consumers, p. 164–195. *In* V. H. Resh and D. M. Rosenberg [ed.] The ecology of aquatic insects. Prager Science, New York, NY.

Mason, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. J. Wildl. Manage. 40: 775–788.

Menzel, D. W., and R. F. Vaccaro. 1964. The measurement of dissolved organic and particulate carbon in seawater. Limnol. Oceanogr. 9: 138–142.

Merritt, R. W., and K. W. Cummins [ed.] 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Co., Dubuque, IA. 441 p.

Mundie, J. H. 1969. Ecological implications of the diet of juvenile coho in streams, p. 135–152. *In* T. G. Northcote [ed.] Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C. 388 p.

1974. Optimization of the salmonid nursery stream. J. Fish. Res. Board Can. 31: 1827–1837.

Mundie, J. H., S. M. McKinnel, and R. E. Traber. 1983. Responses of stream zoobenthos to enrichment of gravel substrates with cereal grain and soybean. Can. J. Fish. Aquat. Sci. 40: 1702–1712.

Murphy, M. L. 1984. Primary production and grazing in freshwater and intertidal reaches of a coastal stream, Southeast Alaska. Limnol. Oceanogr. 29: 805–815.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon, Can. J. Fish. Aquat. Sci. 38: 137–145.

Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. Am. Fish. Soc. 110: 469–478.

Murphy, M. L., and W. R. Meehan. 1991. Stream ecosystems. Am. Fish. Soc. Spec. Publ. 19: 17–46.

Naiman, R. J., and J. R. Sedell. 1979. Relationships between metabolic parameters and stream order in Oregon. Can. J. Fish. Aquat. Sci. 37: 834–847.

Perrin, C. J., M. L. Bothwell, and P. A. Slaney. 1987. Experimental enrichment of a coastal stream in British Columbia: effects of organic and inorganic additions on autotrophic periphyton production. Can. J. Fish. Aquat. Sci. 44: 1247–1256.

Peterman, R. M. 1982. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. Can. J. Fish. Aquat. Sci. 39: 904–913.

Peterson, N. P. 1982. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. Can. J. Fish. Aquat. Sci. 39: 1308–1310.

Schasse, H. W. 1987. Geologic map of the Centralia Quadrangle, Washington. Washington Div. of Geol. and Earth Resour., Open File Rep. 87-11, Olympia, WA.

Scrivener, J. C., and M. J. Brownlee. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 46: 681–696.

Shortreed, K. R. S., and J. G. Stockner. 1982. The impact of logging on periphyton biomass and species composition in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia, p. 197–209. *In* G. F. Hartman [ed.]. Proceedings of the Carnation Creek Workshop, a 10 year review. Pacific Biological Station, Nanaimo, B.C. 404 p.

Stockner, J. G., and K. R. S. Shortreed. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. J. Fish. Res. Board Can. 33: 1553–1563.

1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. J. Fish. Res. Board Can. 35: 28–34.

Triska, F. J., J. H. Duff, and R. J. Avazino. 1989. Influence of exchange flow between the channel and hyporheic zone on nitrate production in a small mountain stream. Can. J. Fish. Aquat. Sci. 47: 2099–2111.

Triska, F. J., J. R. Sedell, and B. Buckley. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: II. Biochemical and nutrient changes. Verh. Int. Ver. Limnol. 19: 1628–1639.

Triska, F. J., J. R. Sedell, and S. V. Gregory. 1982. Coniferous forest streams, p. 292–332. *In* R. L. Edmonds [ed.] Analysis of coniferous forest ecosystems in the western United States. United States International Biological Program Synthesis Series 14. Hutchinson Ross, Stroudsburg, PA.

Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. BioScience 25: 376–381.

Vollenweider, R. A. [ed.] 1974. A manual on methods for measuring primary production in aquatic environments. International Biological Program Handbook 12, 2nd ed. Blackwell Science Publishers, London. 285 p.

Wallace, J. B., and M. E. Gurtz. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. Am. Midl. Nat. 115: 25–41.

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Can. J. Fish. Aquat. Sci. 45: 1110–1122.

Warren, C. E., J. H. Wales, G. E. Davis, and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. J. Wildl. Manage. 28: 617–660.

Weber, P. K. 1981. Comparisons of the lower trophic levels of small stream communities in forest and clearcut sites, southeast Alaska. Ph.D. thesis, University of Washington, Seattle, WA.

Wetzel, R. G., and G. E. Likens. 1979. Limnological analyses. W. B. Saunders, Philadelphia, PA. 357 p.

Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Can. J. Fish. Aquat. Sci. 42: 1668–1672.

Generality of Microhabitat Suitability Models for Young Colorado River Cutthroat Trout (*Oncorhynchus clarki pleuriticus*) across Sites and among Years in Wyoming Streams

Michael A. Bozek[1] and Frank J. Rahel

Department of Zoology and Physiology, University of Wyoming, Box 3166, Laramie, WY 82071, USA

Bozek, M. A., and F. J. Rahel. 1992. Generality of microhabitat suitability models for young Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) across sites and among years in Wyoming streams. Can. J. Fish. Aquat. Sci. 49: 552–564.

The generality of microhabitat-use and preference models for young-of-year (YOY) Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) was tested across sites and years among geomorphically different streams. Depths, velocities, and substrate types used by YOY cutthroat trout often differed across both sites and years. These differences could only partially be explained as a result of differences in microhabitat availability. Microhabitat-use and preference models also varied in their ability to predict the amount of suitable microhabitat across sites. Estimates of suitable microhabitat abundance differed by up to 40% when microhabitat models were randomly used across sites. However, use of a composite model resulted in estimates of suitable microhabitat abundance that differed by less than 20% of that estimated by site-specific models. Therefore, composite models developed for a region may be a useful approach for assessing microhabitat when development of site-specific microhabitat models is not possible. We recommend that further assessment of model generality be conducted for other life stages and species prior to applying microhabitat models to sites other than those where the models were developed.

Les auteurs ont vérifié le caractère général de modèles d'utilisation et de préférence d'habitats dans le cas des truites fardées (*Oncorhynchus clarki pleuriticus*) de moins d'un an du fleuve Colorado, soit entre les sites et entre les années dans des cours d'eau géomorphologiquement différents. La profondeur, la vitesse du courant et le type de substrat recherchés par les truites fardées de moins d'un an ont souvent varié entre les sites et les années. La disponibilité de microhabitats ne peut qu'en partie expliquer ces différences. Les modèles d'utilisation et de préférence d'habitats ont aussi varié dans leur capacité de prévoir le nombre de microhabitats adéquats aux divers sites. Les estimations de ce nombre variaient jusqu'à 40 % lorsque des modèles de microhabitat étaient appliqués aléatoirement aux divers sites. Toutefois, l'utilisation d'un modèle polyvalent d'une région peut servir d'approche utile à l'évaluation de microhabitats lorsque l'élaboration de modèles de microhabitats particuliers n'est pas possible. Les auteurs recommandent qu'une évaluation ultérieure du caractère général de tels modèles soit effectuée dans le cas d'autres stades vitaux et d'autres espèces avant d'appliquer des modèles de microhabitat à des sites autres que ceux à l'origine des modèles.

Received January 29, 1991
Accepted October 4, 1991
(JA882)

Reçu le 29 janvier 1991
Accepté le 4 octobre 1991

Habitat models have become an integral part of fisheries management. Microhabitat models, a subset of habitat models, are histograms or curves that quantify microhabitat requirements (e.g. depth, velocity, substrate, cover) of stream fish. In application, microhabitat models are used in streams where they are linked to hydraulic models in order to estimate the quantity of microhabitat available to individual species (Stalnaker 1979; Bovee 1982; Shirvell 1989). Early modeling efforts, however, were hampered because the microhabitat requirements of many species of fish were unknown (Stalnaker 1979; Orth et al. 1981). But since then, many microhabitat models have been developed (see Bovee 1986; Bovee and Zuboy 1988) and the use of these models to quantify stream microhabitat for various fish species has increased (Conder and Annear 1987; Orth 1987).

Proper use of microhabitat models in modeling efforts is based upon three critical assumptions: (1) that microhabitat used by fish represents the preferred microhabitat of the fish, (2) that fish select the optimal microhabitat for growth and survival, and (3) that microhabitat preferences are characteristic of the species and, therefore, microhabitat models for that species are transferable among streams (Baltz et al. 1987). The extent to which microhabitat models are characteristic of a species and thus transferable among streams, however, is not well known (Moyle and Baltz 1985; Morin et al. 1986; Orth 1987) and tests of the generality of microhabitat models appear to be infrequent.

Microhabitat use by a single species of fish may differ for many reasons including changes in seasonal habitat requirements (Sheppard and Johnson 1985; Hillman et al. 1987; Baltz et al. 1991), differences in available microhabitat among streams (Shirvell 1989), changes in food availability (Wilzbach and Cummins 1986), or as a result of intra- and interspecific competition (Schlosser 1987). Regardless of the reasons for differences in microhabitat use, researchers have suggested using microhabitat models developed specifically for each stream in order to minimize problems associated with the potential lack of model generality across sites (Moyle and Baltz 1985; DeGraaf and Bain 1986; Gore and Nestler 1988; Shirvell 1989). However, development of numerous site-specific microhabitat models is costly and time consuming. Therefore, the ability to use general models across sites is highly desirable, yet testing of model generality is needed in order to understand the limitations of across-stream use of microhabitat models (Morin et al. 1986; Beecher 1987; Shirvell 1989).

---

[1] Present address: Ontario Ministry of Natural Resources, Fisheries and Tourism Research Unit, Centre for Northern Forest Ecosystem Research, Lakehead University, 955 Oliver Road, Thunder Bay, Ont. P7B 5E1, Canada.

We initiated modeling efforts to assess the impacts from water development on Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in Wyoming streams. Habitat for the Colorado River cutthroat trout has been extensively modified and this subspecies presently occupies less than 1% of its original range (Behnke 1979). Remaining populations continue to be threatened by water development activity. However, streams where these trout occur are geomorphically diverse, and thus, the potential existed that microhabitat use might also differ across streams. This research provided an opportunity to develop microhabitat suitability models on seven different streams and to assess their generality across streams and years. The purpose of our study was to (1) quantify the microhabitat available to, and used by, young-of-year (YOY) Colorado River cutthroat trout (hereafter referred to as cutthroat trout), (2) develop microhabitat preference models for YOY cutthroat trout, and (3) evaluate the generality of the microhabitat use models across a variety of stream types.

Materials and Methods

Study Area

Cutthroat trout occur in the Little Snake River drainage and the Green River drainage in Wyoming. The drainage is located in south-central Wyoming (Carbon County) on the west side of the continental divide in the Sierra Madre Mountains. The headwaters originate from snowmelt and springs at an elevation of 3050 m in the Huston Park Wilderness Area. Precipitation occurs largely as snow, with peak runoff occurring from May through late June. The drainage is protected from upstream migration of nonnative salmonids and other species by a man-made migration barrier. The only other fish species present in the drainage is mottled sculpin (*Cottus bairdi*) which was present only at one site. In the Little Snake River drainage, our sampling focused on the North Fork Little Snake River, a 28-km tributary that contains the largest contiguous population of the subspecies in Wyoming (Binns 1977) (see Bozek 1990 for specific locations).

The Green River drainage is located in southwestern Wyoming with headwaters in the Wind River Mountains, north of Pinedale, Wyoming. Tributary streams join the Green River from both the Wind River (east) and Wyoming (west) mountain ranges. Cutthroat trout here exist only as disjunct remnant populations that are found upstream of natural and man-made migration barriers. Cutthroat trout have been displaced from downstream habitats and unprotected headwater reaches by brook trout (*Salvelinus fontinalis*) (Binns 1977) and possibly by rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). However, cutthroat trout was the only species of salmonid occurring within our study reaches. Mottled sculpins, the only other fish species present at the study sites, were rare.

Study Design and Methodology

Microhabitat used by cutthroat trout (0–2 mo postemergence) was measured at seven sites during 3 yr (Table 1). Each site was 100 m in length and was located on either first- or second-order streams that differed considerably in location, elevation, and geomorphology. Two sites in the North Fork Little Snake River drainage (Deadman Creek and Harrison Creek) were sampled each year from 1987 to 1989. In 1987, two additional sites were sampled within the North Fork Little Snake River drainage (headwaters of the North Fork Little Snake River and Green Timber Creek). In addition to the sites in the North Fork Little Snake River that were sampled, three additional sites were sampled in the upper Green River drainage: Lead and Rock Creek in 1988 and Willow Creek in 1989.

Sampling methodology was standardized in several ways. First, sites were selected only if cutthroat trout was the only salmonid species present in order to avoid habitat shifts caused by interspecific interactions among salmonid species. Second, microhabitat-use data were collected only between 09:00 and 16:00 Mountain Standard Time and only after water temperatures warmed to a minimum of 5°C. Third, surveys were conducted only after 100% emergence of cutthroat trout alevins had occurred. This was verified by gently removing gravel from redds and searching for eggs and alevins at each site. Emergence of cutthroat trout in the North Fork Little Snake River extends over a 2-mo period and was complete by early August during all 3 yr of the study. Emergence of cutthroat trout in the Green River drainage was also complete by early August.

Habitat-use information at each site was collected by two people making observations of fish positions from the streambank. Streambank observations were used because the shallow depth of these streams precluded the use of underwater observations (Bozek and Rahel 1991). Observers wore cryptic clothing and their observations appeared to cause minimal disturbance to fish. In fact, disturbances needed to be flagrant to elicit responses from young fish, as only 50% of intentionally disturbed fish (e.g. two hand waves directly over fish position) sought cover (Bozek and Rahel 1991). Therefore, positions of observed fish were considered accurate.

Observations of fish positions were made for the entire 100-m stream segment, working in an upstream direction. The stream segment was divided into pool–riffle reaches for observation purposes. Both observers stopped at each stream reach and remained stationary for 5 min while observing fish positions. After 5 min, the positions of undisturbed fish were noted. These positions were then marked with rods at locations that were visually isolated from upstream areas. Observers then continued working upstream. Within an hour, water depth, nose velocity, and substrate associated with fish positions were measured at the locations marked by the rods. Velocity was measured with a Marsh-McBirney model 201 current meter with an accuracy to 0.01 m/s (Marsh-McBirney, Gaithersburg, MD).

Twenty to 25 YOY cutthroat trout were measured immediately following completion of microhabitat observations at each site. Fry were placed on their side in a moistened petri dish and quickly measured using a small, flat plastic ruler placed beneath the petri dish. Total length was measured from the tip of the snout to the tip of the caudal fin. During the three years of this study, mean total lengths (±1 SE) of YOY cutthroat trout ranged from 22.7 ± 0.52 to 33.8 ± 0.39 mm among sites.

TABLE 1. Habitat characteristics of sites used to examine microhabitat use by YOY cutthroat Trout in Wyoming streams. Depth, velocity, and stream width are mean values (ranges in parentheses). NFLSR = North Fork Little Snake River.

Site	Drainage	Elevation (m)	Slope (%)	Depth (cm)	Velocity (m/s)	Discharge (m^3/s)	Stream width (cm)	*n* used^a	*n* available^b
1987									
NFLSR	NFLSR	2761	2	15.1 (1–76)	0.05 (0–0.36)	0.004	266	66	712
Deadman	NFLSR	2609	12	7.8 (1–58)	0.09 (0–0.87)	0.016	282	110	865
Green Timber	NFLSR	2533	3	8.6 (1–38)	0.06 (0–0.35)	0.005	204	70	692
Harrison	NFLSR	2530	11	5.8 (1–30)	0.05 (0–0.52)	0.005	273	179	297
1988									
Deadman	NFLSR	2609	12	8.8 (1–46)	0.08 (0–0.68)	0.023	311	85	266
Harrison	NFLSR	2530	11	5.6 (1–27)	0.07 (0–0.40)	0.005	249	174	265
Lead	Green River	2475	2	10.0 (1–41)	0.22 (0–0.83)	0.031	233	143	293
Rock	Green River	2300	4	9.7 (1–40)	0.25 (0–1.18)	0.030	149	103	268
1989									
Deadman	NFLSR	2609	12	11.0 (1–61)	0.14 (0–0.91)	0.036	321	62	222
Harrison	NFLSR	2530	11	6.8 (1–27)	0.10 (0–0.57)	0.018	282	156	284
Willow	Green River	2580	4	5.5 (1–33)	0.10 (0–0.65)	0.010	216	92	241

[a] *Number of observations used to assess habitat use.*
[b] *Number of transect points used to assess available habitat.*

Availability of microhabitat at each site was quantified using transects and was completed within 1 d of collecting microhabitat-use data. Each 100-m site was divided into 10-m segments. Three to four transects were randomly placed within each segment and microhabitat (water depth, mean water column velocity, and substrate) was measured at 10 equally spaced points along each transect. Substrate categories 1–9 indicate detritus (unidentifiable decomposed organic matter), silt (<0.06 mm), sand (0.06–4.7 mm), small gravel (4.8–25.4 mm), large gravel (25.5–76.0 mm), rubble (76.1–304.9 mm), small boulders (305.0–609.9 mm), large boulders (>610.0 mm), and woody debris (identifiable sticks, twigs, branches, or logs), respectively (see Fig. 3).

Microhabitat Models

Both microhabitat-use and preference models were developed from microhabitat information collected at each site. Microhabitat-use models were developed by calculating the relative frequency of use by cutthroat trout for increments of depth, velocity, and substrate and then assigning suitability values to each increment. For these models, optimal microhabitat was identified as that microhabitat increment having the highest frequency of use and was assigned a suitability of 1.0. Observed frequencies for all other increments were then divided by the frequency identified as optimal microhabitat in order to determine each of their suitabilities. This resulted in a normalized scale of suitabilities ranging from 0 to 1.0, with 0 indicating unused microhabitat and 1.0 indicating optimal microhabitat Suitability data were then plotted in a histogram and fitted with a curve. Fitting was accomplished by identifying the first occurrence (i.e. first microhabitat increment) and the last occurrence of each suitability value in the histogram. These suitability values were then used to visually plot a smooth curve.

We developed microhabitat preference models for each site by using logistic regression to describe the relationship between microhabitat use and microhabitat availability (Engelmann 1985; Thielke 1985). Logistic regression has been successfully used in other habitat selection studies (Fenwick 1983; Gerhardt and Hubert 1990). Raw preferences were also calculated. Preference (expressed as the relative probability of use) was computed as a ratio between microhabitat use and microhabitat availability (Voos 1981). Preferences were normalized to suitability values between 0 and 1, with 1 representing optimal microhabitat (i.e. the microhabitat increment having the highest ratio of used to available microhabitat) and 0 representing unused microhabitat.

Data for each microhabitat variable were analyzed by multiple stepwise logistic regression (Program PLR of the Biomedical Computer Programs-BMDP; Engelmann 1985). Each preference model was developed from a regression line using the variable and its squared term in the stepwise regression procedure. Observations of used and available microhabitat were assigned a value of 1 and 0, respectively, and used as the dependent variable. Regression coefficients were used only when $P \leqslant 0.05$. The fit of each regression line to the data was assessed using the C. C. Brown goodness-of-fit test (Engelmann 1985). The regression line having the best fit was used as the preference model.

Statistical Analyses and Model Comparisons

The generality of microhabitat models across sites was examined both statistically and by using each model to estimate the amount of suitable microhabitat present at each site. The distributions of water depths and current velocities that were used by and available to cutthroat trout at each site were compared using the Kolmogorov–Smirnov two-sample test (Sokal and Rohlf 1981; SPSSX 1988). For all tests, alpha was set at 0.05. Reduced alpha levels ($P = 0.05/n$, where n = number of pairwise comparisons) were used to correct for experiment-wise error (Snedecor and Cochran 1980). Comparisons were made (1) between sites sampled within each year, (2) between use and available microhabitat for each site, and (3) between years on the sites sampled during the 3-yr study period. Differences in distributions of substrate categories were analyzed using the log-likelihood ratio test (*G*-test) (Sokal and Rohlf 1981).

To further examine the generality of the microhabitat-use and preference models, we determined how well each model estimated the amount of suitable microhabitat across all study sites.

If the amount of suitable microhabitat estimated by all microhabitat models was similar at a site, then generality was considered high. We defined suitable microhabitat as those transect locations in each stream where both the depth and velocity had a suitability value of 0.5 or greater based upon the microhabitat model (i.e. microhabitat-use or preference model) being tested. The suitability level (0.5) was subjectively chosen for comparison purposes.

Estimates of suitable microhabitat were compared in three ways in order to assess model generality. First, previous investigators have suggested that site-specific models are the best models to use for predicting suitable microhabitat (Moyle and Baltz 1985; Shirvell 1989). Therefore, at each site, an estimate of suitable microhabitat was obtained using the site-specific model and then compared with estimates made using each of the microhabitat models that were developed at other sites. All 11 sites were tested in this manner. Assuming that site-specific models are the best models to use, this comparison assessed how close models from other sites estimated the amount of suitable microhabitat relative to site-specific models.

Second, because site-specific microhabitat models are often not available to use, we compared the maximum difference in estimates of suitable microhabitat that could be obtained when randomly applying microhabitat models (other than a site-specific model) across sites. This test assessed the maximum error that could result if two different individuals were to estimate the amount of suitable microhabitat at a site and the individuals used the two most different microhabitat models that were developed at other sites.

Lastly, we tested the assumption that an ''average microhabitat model'' might be more general than any one individual microhabitat model. Therefore, a composite model was constructed by averaging and then normalizing (to 1.0) the suitabilities of all microhabitat models to determine if a single model could be used across all sites. The estimates from the composite model were then compared with estimates of suitable microhabitat made by each site-specific model.

Results

Habitat Use Across Sites

Depths

The distribution and range of water depths available to YOY cutthroat trout varied considerably among sites (Fig. 1). Three distributions were significantly different for 11 of 15 pairwise site comparisons made within years (Table 2).

Young cutthroat trout were selective in the depths used at each site (Fig. 1). Young cutthroat trout generally used depths from 3 to 20 cm. However, the distributions of depths used were different among 8 of 15 pairwise site comparisons (Table 2). Similarity of available depths between sites had little influence on the similarity of depths used by young trout at those sites. Young trout used significantly different depths at two of four sites where available depth distributions were similar. Conversely, young trout used similar depths at 5 of 11 sites where distributions of available depths were significantly different.

The distribution of depths used by young cutthroat trout was significantly different from the distribution of depths available at nearly all sites (Table 3). The preference models derived for each study site using logistic regression supported observations that young cutthroat trout selected deeper water at a higher frequency than would be expected by random use of available depths (Fig. 1). Sites with the greatest mean depth, such as Lead Creek and Rock Creek, showed a high proportion of young cutthroat trout using deeper water. Preference models indicated that optimal depths (where the suitability = 1.0) increased with mean site depth, from about 10 cm at Willow Creek to over 30 cm at Rock Creek (Fig. 1).

Velocity

Velocities available to young cutthroat trout ranged from 0 m/s at all sites to 1.4 m/s at Lead Creek. Distributions of velocities, however, were generally skewed toward slower current speeds at all sites (Fig. 2). The distributions of velocities available to young trout were significantly different in 9 of the 15 pairwise site comparisons (Table 2).

Current velocities used by young cutthroat trout ranged from 0 to 0.35 m/s, but were generally less than 0.06 m/s despite the availability of faster velocities at all sites. During 1987, current velocities used by young trout were not significantly different between any sites despite differences in availability among these sites (Table 2). In 1988, there were significant differences in velocities used for five of six pairwise site comparisons and in 1989 for two of three pairwise site comparisons.

The distributions of velocities used by YOY cutthroat trout were significantly different from the distributions of velocities available at 9 of 11 sites (Table 3). Whereas the use of depth by young cutthroat trout appeared to be constrained by the availability of deep water at each site, velocities used were consistently a narrow subset of slower velocities available at each site (<0.07 m/s). As a result, preference models for velocity were similar among sites because young trout consistently selected these slower water velocities (Fig. 2).

Substrate

Distributions of substrate types available differed significantly among all sites (Fig. 3; Table 2). While most sites had a large proportion of fine sediment (substrate size categories 1–3), Deadman Creek and Green Timber Creek also had a higher proportion of larger substrate sizes than most other sites.

Substrates found in association with YOY cutthroat trout locations differed significantly in 14 of 15 pairwise comparisons (Table 2). Although there was a general trend for young trout to be found over smaller substrates (silt and sand), substrate selection was highly variable among sites (Fig. 3).

Substrates found in association with young cutthroat trout locations differed significantly from the distribution of substrates available at all sites (Table 3). At several sites (Deadman Creek, Lead Creek, Rock Creek), YOY cutthroat trout used fine substrates in higher proportion than their availability. At other sites, the opposite was true, with cobble substrates receiving considerable use. Young cutthroat trout also used woody debris in higher proportion than its availability at several sites.

Habitat Use Across Years

Depth

For Deadman Creek, the distributions of depths available to YOY cutthroat trout were significantly different between 1987 and 1989 and between 1988 and 1989 (Table 4). This was concurrent with differences in discharge among years (Table 1). For Harrison Creek, the distributions of depths available to young trout were significantly different between 1988 and 1989. This was also concurrent with differences in discharge between

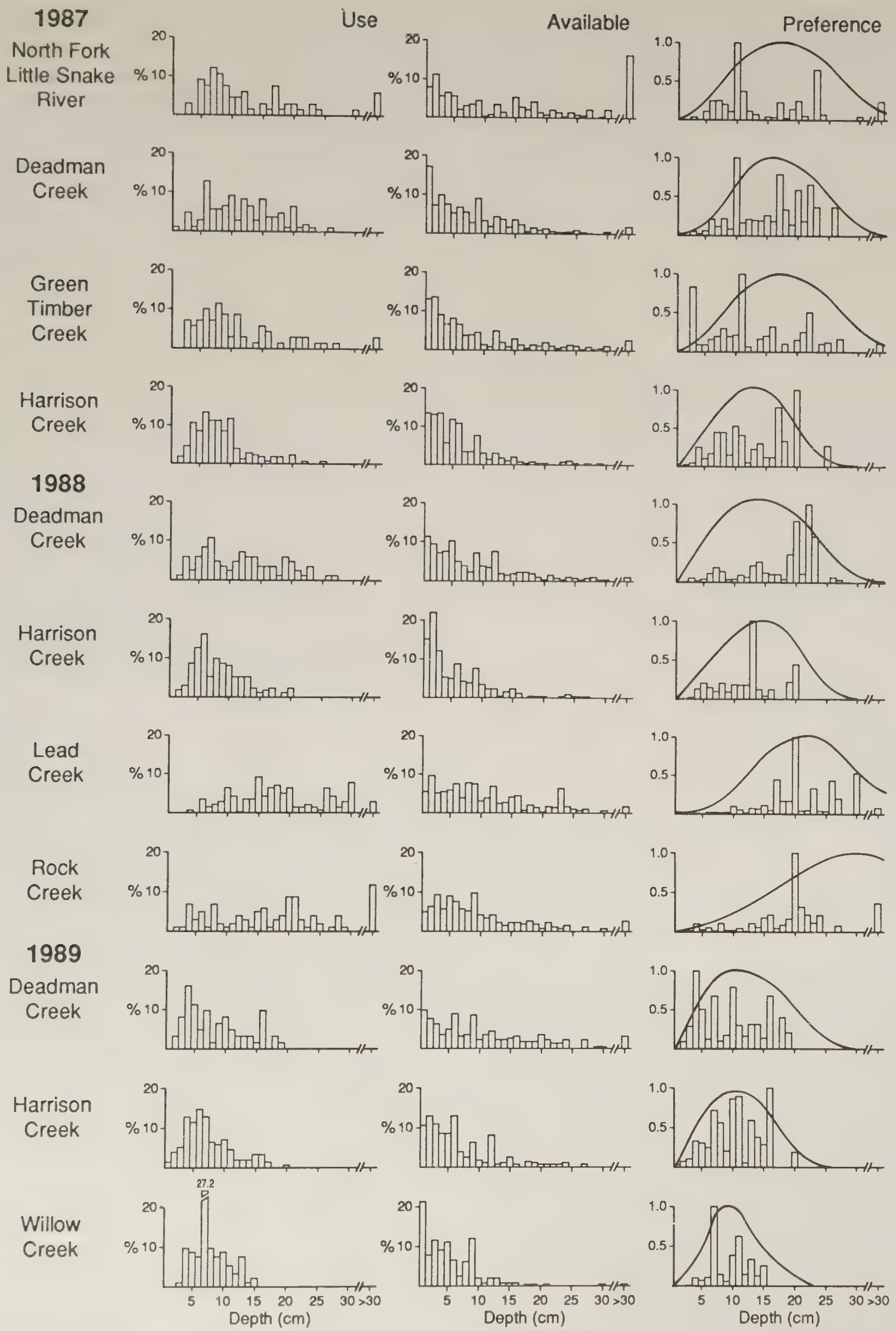


FIG. 1. Water depths used by, available to, and preferred by YOY cutthroat trout at each site during the 3 yr of the study. Preference, as determined by logistic regression, is plotted as a solid line in the histograms.

TABLE 2. Differences between sites in the distributions of depths, velocities, and substrates that were used by and available to YOY cutthroat trout. NFLSR = North Fork Little Snake River. An asterisk (*) indicates a significant difference based upon $P = 0.05/n$, where n = number of pairwise tests within each year.

		Available microhabitat			Microhabitat use		
Year	Site-by-site comparison	Depth P	Velocity P	Substrate P	Depth P	Velocity P	Substrate P
1987	Deadman vs. Harrison	<0.001*	<0.001*	<0.001*	<0.001*	0.077	<0.001*
	Deadman vs. NFLSR	<0.001*	<0.001*	<0.001*	0.710	0.020	<0.001*
	Deadman vs. Green Timber	0.049	<0.001*	<0.001*	0.123	0.055	0.003*
	Harrison vs. NFLSR	<0.001*	<0.001*	<0.001*	0.002*	0.325	<0.001*
	Harrison vs. Green Timber	<0.001*	0.358	<0.001*	0.024	0.221	<0.001*
	NFLSR vs. Green Timber	<0.001*	<0.001*	<0.001*	0.746	0.912	<0.001*
1988	Deadman vs. Harrison	<0.001*	0.730	<0.001*	<0.001*	<0.001*	<0.001*
	Deadman vs. Lead	0.008*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	Deadman vs. Rock	0.111	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	Harrison vs. Lead	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	Harrison vs. Rock	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	Lead vs. Rock	0.680	0.402	<0.001*	0.074	0.856	<0.001*
1989	Deadman vs. Harrison	<0.001*	0.052	<0.001*	0.371	0.508	0.021*
	Deadman vs. Willow	<0.001*	0.023	<0.001*	0.132	<0.001*	<0.001*
	Harrison vs. Willow	0.060	0.482	<0.001*	0.007*	<0.001*	<0.002*

TABLE 3. Results indicating at which sites YOY cutthroat trout used distributions of depths, velocities, and substrates that were significantly different than those available. NFLSR = North Fork Little Snake River. An asterisk (*) indicates a significant difference based upon $P = 0.05/n$, where n = number of pairwise tests within each year.

Year	Site	Depth P	Velocity P	Substrate P
1987	NFLSR	<0.001*	0.425	<0.001*
	Deadman	<0.001*	<0.001*	<0.001*
	Green Timber	<0.001*	0.016	0.036
	Harrison	<0.001*	<0.001*	<0.001*
1988	Deadman	<0.001*	<0.001*	<0.001*
	Harrison	<0.001*	<0.001*	<0.001*
	Lead	<0.001*	<0.001*	<0.001*
	Rock	<0.001*	<0.001*	<0.001*
1989	Deadman	0.097	<0.001*	<0.001*
	Harrison	<0.001*	<0.001*	<0.001*
	Willow	<0.001*	<0.001*	<0.001*

those two years. During 1987 and 1988, discharges were similar and there were no differences between these years.

The distributions of depths used by young cutthroat trout in Deadman Creek were significantly different between 1987 and 1989 (Table 4). These were the same years that the distribution of depths available to young differed. For Harrison Creek, there were no significant differences in depths used between years even though availability of depths differed between 1988 and 1989.

Depth preference models appeared to be similar among years at both Deadman Creek and Harrison Creek (Fig. 1). While depths preferred at Deadman Creek in 1989 differed slightly from the previous 2 yr, the differences were relatively minor. At Harrison Creek, depths preferred were similar for all 3 yr.

Velocity

The distributions of velocities available to YOY cutthroat trout in Deadman Creek were significantly different between 1987 and 1989 and between 1988 and 1989 (Table 4). For Harrison Creek, the distributions of velocities were not significantly different between 1987 and 1988, but differed between 1987 and 1989 and between 1988 and 1989.

The distributions of velocities used by young trout in Deadman Creek were significantly different between 1987 and 1988

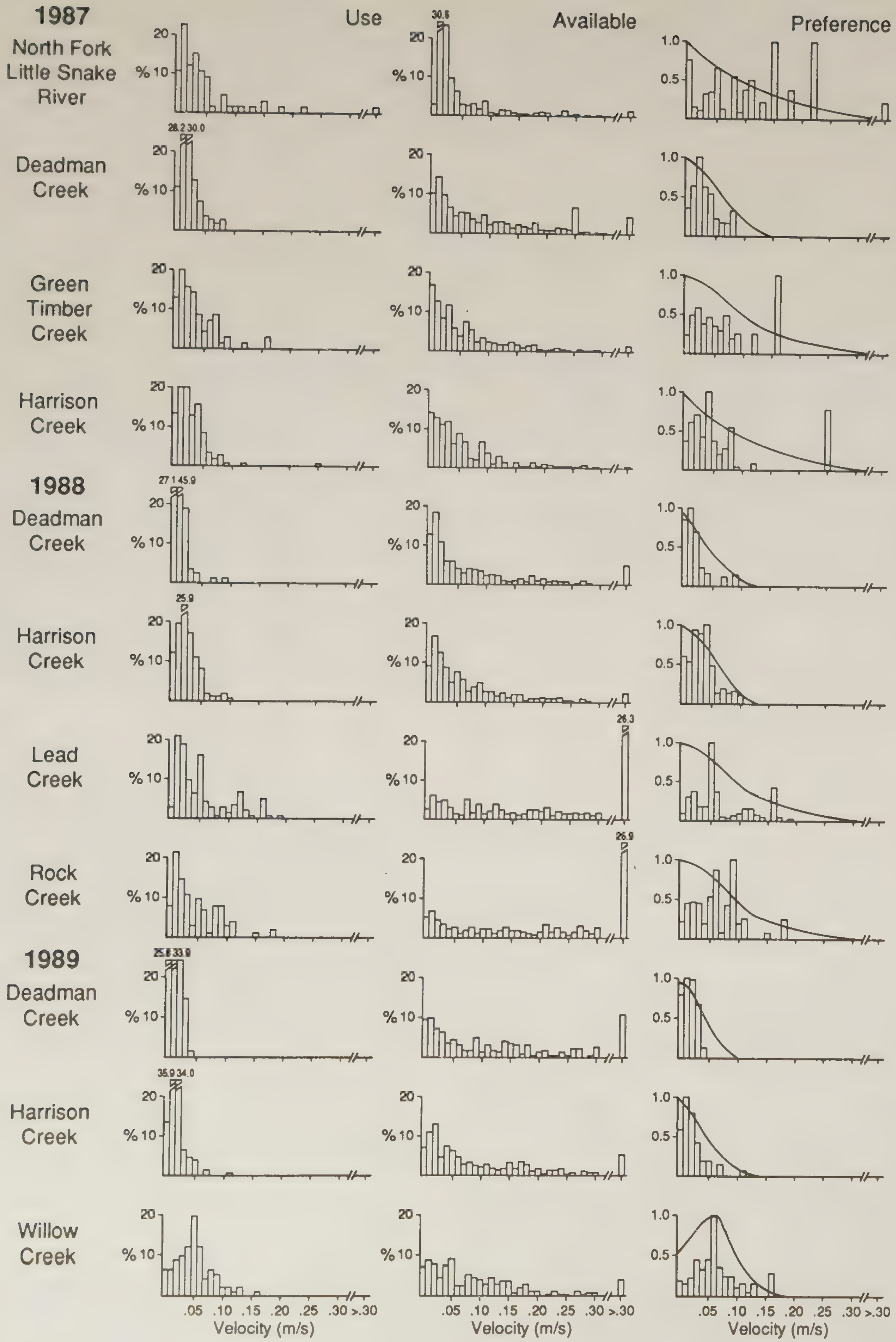


FIG. 2. Water velocities used by, available to, and preferred by YOY cutthroat trout at each site during the 3 yr of the study. Preference, as determined by logistic regression, is plotted as a solid line in the histograms.

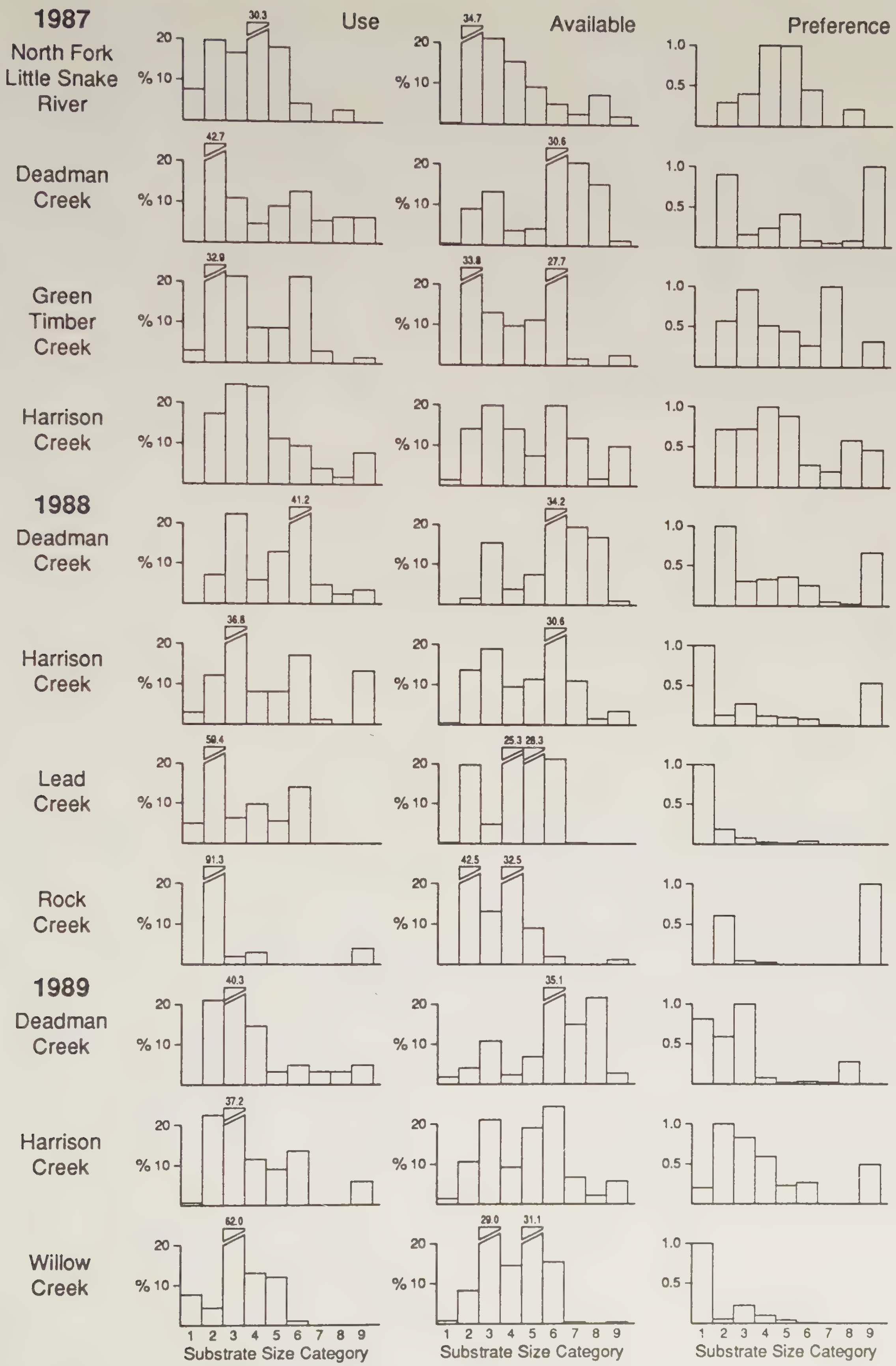


FIG. 3. Substrates used by, available to, and preferred by YOY cutthroat trout at each site during the 3 yr of the study.

TABLE 4. Differences between years in the distributions of depths, velocities, and substrates available and used at Deadman and Harrison creeks. An asterisk (*) indicates a significant difference based upon $P = 0.05/n$, where n = number of pairwise tests per site. Details on statistical tests are given in the text.

		Available microhabitat			Microhabitat use		
Site	Years compared	Depth *P*	Velocity *P*	Substrate *P*	Depth *P*	Velocity *P*	Substrate *P*
Deadman	1987–1988	0.274	0.071	<0.001*	0.905	0.001*	<0.001*
	1988–1989	0.001*	<0.001*	<0.001*	0.024	0.554	0.027
	1987–1989	0.001*	<0.001*	<0.001*	0.002*	0.069	<0.001*
Harrison	1987–1988	0.098	0.440	<0.001*	0.713	0.588	0.005*
	1988–1989	0.006*	0.005*	0.019*	0.048	<0.001*	0.056
	1987–1989	0.426	<0.001*	<0.001*	0.150	<0.001*	<0.001*

TABLE 5. Range of depths and velocities that have a suitability ≥0.5 based on site-specific habitat-use and preference models that have been normalized to 1.0. NFLSR = North Fork Little Snake River.

		Habitat-use models		Preference models	
Year	Site	Depth (cm)	Velocity (m/s)	Depth (cm)	Velocity (m/s)
1987	NFLSR	5–17	0–0.04	5–28	0–0.11
	Deadman	6–20	0.01–0.02	8–25	0–0.05
	Green Timber	3–15	0–0.07	6–29	0–0.10
	Harrison	4–10	0–0.04	5–21	0–0.06
1988	Deadman	3–14	0–0.01	6–27	0–0.03
	Harrison	4–10	0.01–0.05	5–20	0–0.07
	Lead	10–30	0.01–0.05	12–39	0–0.13
	Rock	6–34	0.01–0.03	12–46	0–0.12
1989	Deadman	3–16	0–0.02	3–17	0–0.03
	Harrison	3–7	0–0.02	4–17	0–0.04
	Willow	7	0.03–0.06	5–15	0–0.11

even though the distributions of velocities available to young trout were not significantly different (Table 4). The distribution of velocities used by cutthroat trout was similar between 1987 and 1989 and between 1988 and 1989 even though the distributions of velocities available to young trout were significantly different between those years. For Harrison Creek, the distribution of velocities used by cutthroat trout was significantly different between 1988 and 1989 and between 1987 and 1989.

Velocity preference models appeared similar among years at both Deadman Creek and Harrison Creek (Fig. 2). Optimal velocities at Deadman Creek were consistently less than 0.04 m/s, while those at Harrison Creek were consistently less than 0.06 m/s.

Substrate

The types of substrates available to YOY cutthroat trout were significantly different between all years at both Deadman Creek and Harrison Creek (Table 4). The types of substrates used by young in Deadman Creek were significantly different between 1987 and 1988 and between 1987 and 1989. At Harrison Creek, the categories of substrates were significantly different between 1987 and 1988 and between 1987 and 1989.

Tests of Model Generality

The range of depths and velocities that had microhabitat suitabilities ≥0.5 varied among sites for both microhabitat-use and preference models (Table 5). Suitable depths from preference models were deeper (3–46 cm) than those from microhabitat-use models (3–34 cm) and this trend was consistent across all sites. Suitable velocities from preference models (0–0.14 m/s) were higher than those from microhabitat-use models (0–0.06 m/s) (Table 5). Because preference models predicted a wider range of suitable microhabitat, the amount of suitable area estimated using preference models was usually higher than the amount estimated using microhabitat-use models.

No single microhabitat-use or preference model derived among the study streams was found to be satisfactory for estimating the amount of suitable microhabitat across all sites. Models both overestimated and underestimated the suitable microhabitat that was estimated by the site-specific models (Appendix 1). Comparing microhabitat-use models, 12% of the estimates differed by 20% from those estimates made by site-specific models in study streams and 1% of the estimates differed by over 30% (Appendix 1). Using preference models, 9% of the suitable microhabitat model predictions differed by 20% from predictions made with site-specific models, while none differed by 30% (Appendix 1). However, if estimates of suitable microhabitat from preference models were compared with those derived from site-specific microhabitat-use models or vice versa, the error in the estimates of suitable microhabitat was considerably higher.

In these analyses, model performance was judged by comparing the amount of suitable microhabitat estimated by the site-specific model with the amount estimated by models developed from data at other sites. However, often site-specific models are not available. Therefore, model performance was also judged by comparing the maximum range of suitable microhabitat that could be estimated for each site depending upon which models were used. For example, the amount of suitable microhabitat predicted for Green Timber Creek was 36.4% when the microhabitat-use model developed at Green Timber Creek was used but was as little as 1.2% when the microhabitat-use model developed at Willow Creek was used. Further, the amount of suitable microhabitat was 40.2% when the microhabitat preference model developed at Green Timber Creek was applied to Green Timber Creek.

When using microhabitat-use models at some sites, the range of suitable microhabitat that was estimated was large, with differences as high as from 30 to 50% (Appendix 1). When preference models were used, the range of suitable microhabitat that was estimated was smaller, but still substantial (Appendix 1). Thus, large errors in estimates of suitable microhabitat could result depending upon which microhabitat-use or preference model was used at a particular site. As in the first set of tests, if estimates from microhabitat-use models were compared with those derived from preference models or vice versa, the error in estimates of suitable microhabitat would again be higher.

Lastly, model generality was tested using a composite model. However, a choice first needed to be made regarding whether the microhabitat-use or preference models should be used for the composite model. To do this, the relationships between microhabitat-use models and preference models to the available microhabitat at all sites were closely examined for both variables. In the case of velocity, a wide range of velocities (0 to >0.30 m/s) were available at all sites. However, the range of velocities primarily used by YOY cutthroat trout was consistently less than 0.08 m/s at each site as reflected in the microhabitat-use models. In contrast, the range of suitable velocities in preference models was often much higher than any velocities consistently being used by YOY cutthroat trout in the streams. Therefore, the microhabitat-use models were used to construct the composite model for velocity.

In selecting the composite model for depth, the preference model was chosen because use of deeper water by young fish across sites appeared to be constrained by the ranges of depths available at each site. The trend in use of depth across most sites suggested that YOY cutthroat trout used deeper water as site depth increased (Fig. 1; Table 5). For example, the maximum depth having a suitability ⩾0.5 was 10 cm at Harrison Creek in 1988. Water depths available at this site were among the shallowest across all sites. On the other hand, the shallowest depth having a suitability ⩾0.5 at Lead Creek was 10 cm where considerable deep water was available. Therefore, the preference models were used to construct the composite model for depth.

Estimates of suitable microhabitat made by the composite model (Fig. 4) differed by less than 20% of those estimates made by either the site-specific microhabitat-use or the site-specific preference models at all 11 sites (Appendix 1). Use of the composite model, therefore, appeared to be an alternative to random across-site use of microhabitat models.

Discussion

Our research assessing the generality of microhabitat models for YOY cutthroat trout was conducted in first- and second-order streams having a diverse array of stream habitat conditions. Each model that we constructed provided an opportunity to test an original site-specific model against other models constructed in different habitat conditions. We found significant differences among habitat-use models and visual differences among preference models developed at different sites. Using those models, we also found that estimates of suitable microhabitat might differ by as much as 40% depending upon the model being used, and those estimates could be higher if habitat-use models were compared with preference models. Overall, microhabitat models developed at a variety of sites appeared to be different enough to caution against randomly using them across sites. This was also true of preference models that attempted to correct for site-specific environmental bias.

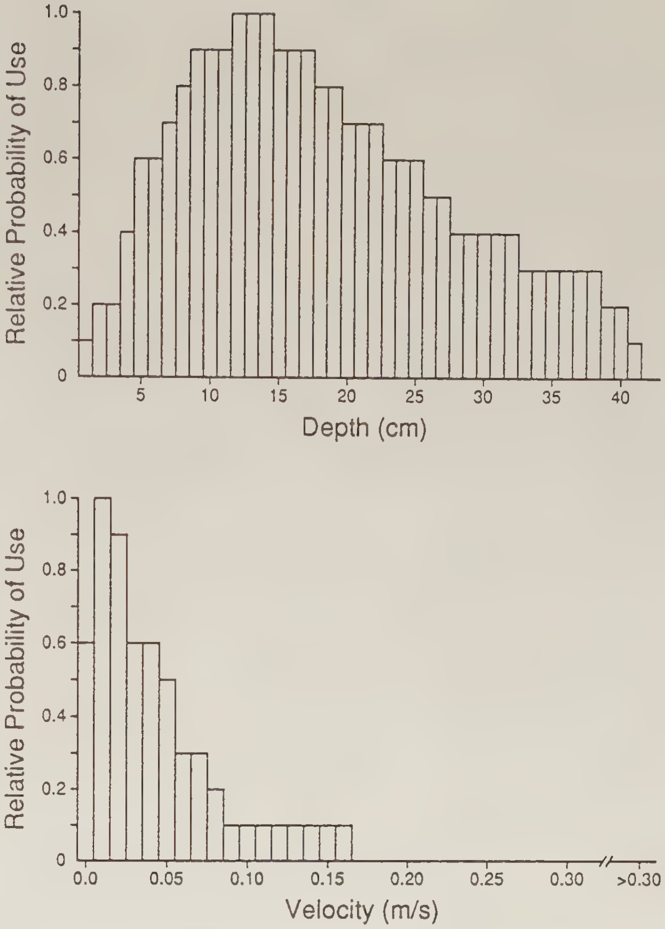


FIG. 4. Composite suitability model of water depth and current velocity for YOY cutthroat trout. Each model is derived from combining all 11 suitability models in this study.

Previous research related to the generality of microhabitat use among stream fish has shown that microhabitat models may indeed differ across sites. Sheppard and Johnson (1985) found differences between site-specific microhabitat models that they developed and general microhabitat models developed by the United States Fish and Wildlife Service for coho salmon (*Oncorhynchus kisutch*). Moyle and Baltz (1985) found differences in microhabitat use for several different species of fish in California streams and believed that the differences resulted from species interactions and differences in microhabitat availability. Shirvell (1989) found that estimates of chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat in the Nechako River in British Columbia differed depending upon the source of the microhabitat model used in the predictions. Shirvell and Dungey (1983) found that microhabitat use of brown trout differed depending upon activity (e.g. feeding versus spawning).

Various explanations have been given for differences in microhabitat use among streams including intra- and interspecific competition (Schlosser 1987; Gatz et al. 1987), seasonal microhabaitat-use shifts (Hillman et al. 1987), size class differences (Moyle and Baltz 1985), and differences in microhabitat availability (DeGraaf and Bain 1986). Because different degrees of interacting factors can influence fish microhabitat use in different streams, and the complexity of such interactions is difficult to elucidate, several investigators have called for the development of site-specific models (Moyle and Baltz 1985; DeGraaf and Bain 1986; Orth 1987; Shirvell 1989). It is believed that site-specific models directly incorporate both the biotic and abiotic factors that may influence microhabitat use within the stream where the model is developed and will be used. As a result, use of site-specific models should reduce the degree of error associated with randomly applying microhabitat models across sites.

The assumption that microhabitat use is characteristic of individual fish species and therefore could be quantified and generalized across streams probably was the basis for the development of a series of general microhabitat models for various species of fish (Bovee and Cochnauer 1977; Bovee 1978). While this assumption has not been adequately tested, these general microhabitat models have received considerable use across streams (Anderson and Nehring 1985; Conder and Annear 1987; Orth 1987), particularly among management agencies and utilities.

In some cases, the trade-off between the time and cost savings gained by using general microhabitat models may not be worth the accuracy lost in using site-specific microhabitat models. Orth (1987) suggested that a critical concern for determining habitat suitability was the abundance of competitors that might influence habitat use and therefore reduce the generality of microhabitat models. Such habitat shifts have been identified in salmonids (Fausch and White 1981; Gatz et al. 1987). However, under some circumstances, applying microhabitat models to streams having similar ranges of habitat conditions and species assemblages appears feasible. Gore and Nestler (1988) suggested that a high degree of generality might be possible among streams having similar habitats. Belaud et al. (1989) verified that microhabitat models developed for brown trout among similar streams could be transferred across sites.

Similar life stages of fish might also allow microhabitat models to be used across streams. Young salmonids, similar to the age that we studied, have narrow ranges of microhabitat requirements (Sheppard and Johnson 1985; DeGraaf and Bain 1986), and therefore, variability among models might be expected to be lower than for adults. As a result, development and use of a composite model might be more practical for a particular life stage such as this, especially when this model is used among streams having similar habitats.

Construction of our composite model required assessing trends in habitat use and availability across 11 sites, which still required considerable work. In our study, the composite model, derived from all of the other models, predicted suitable microhabitat relatively close to site-specific models (<20% difference). Therefore, a composite model may be a reasonable alternative to the costly development of site-specific models, but these models must first be tested prior to use.

Understanding the capabilities and limitations of how accurately microhabitat models reflect microhabitat use, however, is important when applying habitat models across sites. Without testing these models, users cannot determine how accurate the predictions made by models will be when they are applied. This is particularly true when the number of observations on which a model is based is small or when use of the model occurs in situations that differ from the range of conditions that existed where the model was developed (Fausch et al. 1988). Our results suggest that composite models developed for a life stage within a limited geographic region may be a useful compromise between general models that may be inaccurate when applied universally and site-specific models that may only be accurate within a particular stream. More testing on the use of microhabitat models across sites is needed to better understand the degree of variability in models and the reasons for these differences.

Acknowledgments

We thank N. Bozek, M. Bozek, P. Cavalli, L. DeBrey, A. Gripentrog, J. Marr, and S. Wolff for field assistance. We appreciate comments provided by W. Hubert, T. Wesche, L. McDonald, R. Wiley, K. Fausch, and an anonymous reviewer that helped improve the manuscript. Funding was provided by the Wyoming Water Research Center, the Wyoming Game and Fish Department, the University of Wyoming Office of the Vice President for Research, and the University of Wyoming College of Arts and Sciences.

References

ANDERSON, R. M., AND R. B. NEHRING. 1985. Impacts of stream discharge on trout rearing habitat and trout recruitment in the South Platte River, Colorado, p. 59–64. *In* F. W. Olsen, R. G. White, and R. H. Hamre [ed.] Proceedings of the symposium on small hydropower and fisheries. American Fisheries Society, Western Division, Bethesda, MD.

BALTZ, D. M., B. VONDRACEK, L. R. BROWN, AND P. B. MOYLE. 1987. Influence of temperature on microhabitat choices by fishes in a California stream. Trans. Am. Fish. Soc. 116: 12–20.

1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. Trans. Am. Fish. Soc. 120: 166–176.

BEECHER, H. 1987. Simulating trout feeding stations in instream flow models, p. 71–82. *In* J. F. Craig and J. B. Kemper [ed.] Regulated streams: advances in ecology. Plenum Press, New York, NY.

BEHNKE, R. J. 1979. Monograph of the native trouts of the genus *Salmo* of western North America. U.S. Fish Wildl. Serv. Publ. 215 p.

BELAUD, A., P. CHAVEROCHE, P. LIM, AND C. SABATON. 1989. Probability-of-use curves applied to brown trout (*Salmo trutta* Fario L.) in rivers of southern France. Reg. Rivers Res. Manage. 3: 321–336.

BINNS, N. A. 1977. Present status of indigenous population of cutthroat trout, *Salmo clarki*, in southwest Wyoming. Fish. Tech. Bull No. 2. Wyoming Game and Fish Department, Cheyenne, WY.

BOVEE, K. D. 1978. Probability-of-use criteria for the family salmonidae. U.S. Fish Wildl. Serv. Biol. Serv. Prog. FWS/OBS-78/07.

1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Information Paper 12. U.S. Fish Wildl. Serv. Off. of Biol. Serv. FWS/OBS-82/26.

1986. Development and evaluation of habitat suitability criteria for use in the Instream Flow Incremental Methodology. Instream Flow Information Paper 21. U.S. Fish Wildl. Serv. Biol. Rep. 86(7).

BOVEE, K. D., AND T. COCHNAUER. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: fisheries. U.S. Fish Wildl. Serv. Biol. Serv. Prog. FWS/OBS-77/63.

BOVEE, K. D., AND J. R. ZUBOY. [ED.] 1988. Proceedings of a workshop on the development and evaluation of habitat suitability criteria. U.S. Fish Wildl. Serv. Biol. Rep. 88(11).

BOZEK, M. A. 1990. Generality of Habitat models for Colorado River cutthroat trout fry and the influence of adults on habitat choice and behavior. Ph.D. dissertation, University of Wyoming, Laramie, WY. 200 p.

BOZEK, M. A., AND F. J. RAHEL. 1991. Comparison of streamside visual counts to electrofishing estimates of Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) fry and adults. N. Am. J. Fish. Manage. 11: 38–42.

Conder, A. L., and T. C. Annear. 1987. Test of weighted useable area estimates derived from a PHABSIM model for instream flow studies on trout streams. N. Am. J. Fish. Manage. 7: 339–350.

DeGraaf, D. A., and L. H. Bain. 1986. Habitat use by and preferences of juvenile Atlantic salmon in two Newfoundland rivers. Trans. Am. Fish. Soc. 115: 671–681.

Engelmann, L. 1985. PLR 14.5 stepwise logistic regression, p. 330–343. *In* W. J. Dixon [ed.] BMDP statistical software. Department of Biomathematics, University of California, Los Angeles, CA. 725 p.

Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables, 1950–85. Gen. Tech. Rep. PNW-GTR-213. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR. 52 p.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220–1227.

Fenwick, J. W. 1983. Quantifying songbird habitat: a comparison discriminant analysis and logistic regression. M.S. thesis, University of Vermont, Burlington, VT.

Gatz, A. J., M. J. Sale, and J. M. Loar. 1987. Habitat shifts in rainbow trout: competitive influences of brown trout. Oecologia 74: 7–19.

Gerhardt, D. R., and W. A. Hubert. 1990. Spawning habitat of channel catfish in the Powder River system, Wyoming–Montana. Prairie Nat. 22: 155–164.

Gore, J. A., and J. M. Nestler. 1988. Instream flow studies in perspective. Reg. Rivers Res. Manage. 2: 93–101.

Hillman, T. W., J. S. Griffith, and W. S. Platts. 1987. Summer and winter habitat selection by juvenile salmon in a highly sedimented Idaho stream. Trans. Am. Fish. Soc. 116: 185–195.

Morin, A., P. P. Harper, and R. H. Peters. 1986. Microhabitat-preference curves of blackfly larvae (Diptera:Simuliidae): a comparison of three estimation methods. Can. J. Fish. Aquat. Sci. 43: 1235–1241.

Moyle, P. B., and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Trans. Am. Fish. Soc. 114: 695–704.

Orth, D. J. 1987. Ecological considerations in the development and application of instream flow habaitat models. Reg. Rivers Res. Manage. 1: 171–181.

Orth, D. J., R. N. Jones, and O. E. Maughan. 1981. Considerations in the development of curves for habitat suitability criteria, p. 124–133. *In* N. B. Armantrout [ed.] Acquisition and utilization of aquatic habitat inventory information. Western Division American Fisheries Society, Bethesda, MD.

Schlosser, I. J. 1987. The role of predation in age- and size-related habitat use by fish. Ecology 68: 651–659.

Sheppard, J. D., and J. H. Johnson. 1985. Probability-of-use for depth, velocity, and substrate by subyearling coho salmon and steelhead in Lake Ontario tributary streams. N. Am. J. Fish. Manage. 5: 277–282.

Shirvell, C. A., and R. D. Dungey. 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. Trans. Am. Fish. Soc. 112: 355–367.

Shirvell, C. S. 1989. Ability of Phabsim to predict chinook salmon spawning habitat. Reg. Rivers Res. Manage. 3: 277–289.

Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods. Iowa State University Press, Ames, IA.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco, CA.

SPSSX. 1988. Statistical package for the social sciences. SPSS Inc., Chicago, IL.

Stalnaker, C. B. 1979. The use of habitat structure preferenda for establishing flow regimes necessary for maintenance of fish habitat, p. 321–337. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum Press, New York, NY.

Thielke, J. 1985. A logistic regression approach for developing suitability-of-use functions for fish habitat, p. 32–38. *In* F. W. Olsen, R. G. White, and R. H. Hamre [ed.] Proceedings of the symposium on small hydropower and fisheries. American Fisheries Society, Western Division, Bethesda, MD.

Voos, K. A. 1981. Simulated use of the exponential polynomial/maximum likelihood technique in developing suitability of use functions for fish habitat. Ph.D. dissertation, Utah State University, Logan, UT. 85 p.

Wilzbach, M. A., and K. W. Cummins. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology 67: 898–911.

Appendix 1

Table A.1. Percentage of suitable microhabitat occurring at each site as estimated by using each microhabitat model across all sites (predictions are to be compared horizontally for each microhabitat availability site). Two predictions were made at each site. The top value indicates the amount of suitable microhabitat predicted using normalized habitat-use models, while the lower value indicates the amount of suitable microhabitat predicted using normalized preference models. Underlined values are locations where microhabitat use and availability are from the same site. Predictions made by the composite model are given in the last column. Site abbreviations: NFLSR = North Fork Little Snake River; DC = Deadman Creek; GTC = Greek Timber Creek; HC = Harrison Creek; LC = Lead Creek; RC = Rock Creek; WC = Willow Creek.

Sites where suitable microhabitat was estimated	Sites where microhabitat-use data were collected from											Composite model
	1987				1988				1989			
	NFLSR	DC	GTC	HC	DC	HC	LC	RC	DC	HC	WC	
1987												
NFLSR	23.9 47.5	18.5 30.9	30.3 43.2	15.2 36.0	11.5 32.3	15.2 35.4	28.9 41.6	32.6 45.5	20.8 29.2	9.0 27.0	0.8 27.2	40.7
DC	23.6 42.1	12.5 21.6	37.1 36.9	17.5 31.1	15.3 22.7	15.8 32.2	12.1 19.8	17.7 19.4	23.0 29.8	10.4 26.1	0.6 34.8	29.9
GTC	21.7 45.7	9.5 24.3	36.4 40.2	16.5 32.4	12.7 26.6	12.1 34.1	17.1 27.5	20.5 27.5	20.2 28.3	10.1 24.6	1.2 32.4	34.1
HC	28.6 48.8	9.8 20.9	50.2 38.7	25.3 38.0	16.2 21.9	23.2 39.1	12.1 12.5	18.2 12.5	24.6 39.1	16.5 32.0	1.7 44.1	36.7
1988												
DC	28.6 47.0	16.2 23.7	40.2 38.3	21.8 34.2	18.8 25.6	18.4 35.0	17.7 24.1	20.7 23.3	28.2 37.6	13.9 33.5	1.1 34.6	34.6
HC	24.5 40.4	11.3 18.1	43.4 35.8	21.1 33.2	15.5 22.3	21.2 34.7	9.4 10.0	17.7 10.0	24.5 33.2	14.7 28.0	2.3 36.2	30.6
LC	10.2 20.5	4.1 9.9	14.0 17.7	7.2 12.0	4.4 9.0	6.5 14.0	6.5 14.3	7.8 12.6	6.1 12.3	2.1 11.3	0.3 14.3	12.6
RC	8.2 15.7	1.5 5.2	15.7 11.6	9.0 10.0	7.8 5.0	4.5 10.1	2.6 7.5	2.2 5.6	10.5 13.1	7.8 9.7	0.0 13.4	10.1

Table A.1. (*Concluded*)

Sites where suitable microhabitat was estimated	Sites where microhabitat-use data were collected from											Composite model
	1987				1988				1989			
	NFLSR	DC	GTC	HC	DC	HC	LC	RC	DC	HC	WC	
1989												
DC	17.6 37.4	8.1 18.9	23.4 33.8	10.8 26.1	7.7 20.7	9.5 27.0	11.3 24.3	14.4 23.0	14.0 20.3	5.0 18.5	0.5 24.3	26.6
HC	18.7 38.3	11.3 16.2	37.7 31.7	15.5 27.8	10.6 17.6	17.6 28.9	12.3 16.2	15.1 15.5	18.3 26.4	11.6 22.1	0.4 31.7	27.8
WC	14.9 29.5	5.0 11.6	27.4 21.2	14.1 19.5	7.9 9.5	15.4 20.3	5.0 7.5	7.9 7.1	12.5 19.9	7.5 17.4	0.8 28.2	18.6

Diel Pelagic Foraging by a Pandalid Shrimp (*Pandalus montagui*) off Resolution Island (Eastern Hudson Strait)

C. Hudon[1]

Department of Fisheries and Oceans, Science Branch, Arctic Biological Station, 555 Boulevard Saint-Pierre, Ste-Anne-de-Bellevue, Quebec H9X 3R4, Canada

D. G. Parsons

Department of Fisheries and Oceans, Science Branch, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, Nfld. A1C 5X1, Canada

and R. Crawford

Department of Fisheries and Oceans, Science Branch, Freshwater Institute, 501 University Crescent, Winnipeg, Man. R3T 2N6, Canada

Hudon, C., D. G. Parsons, and R. Crawford. 1992. Diel pelagic foraging by a pandalid shrimp (*Pandalus montagui*) off Resolution Island (eastern Hudson Strait). Can. J. Fish. Aquat. Sci. 49: 565–576.

The vertical distribution and diet of shrimp (*Pandalus montagui*) were investigated using a multistage plankton sampler (BIONESS) and were compared with those of shrimp captured on the bottom using a trawl. Massive nocturnal vertical migrations of shrimp were observed in association with intense pelagic feeding activity. The sex ratio, size frequency distribution, and diet of shrimp caught in the water column differed markedly from shrimp caught during their stay on the bottom. Pelagic migrants were mostly males (75%), extending their planktonic foray into morning hours, whereas ovigerous (12%) and nonovigerous (13%) females returned to the bottom at dawn. In the trawl, the representation of males (43%) and ovigerous females (45%) differed, but also fluctuated on a diel cycle. Stomachs of shrimp captured in the BIONESS were fuller and the contents were in better condition than found in shrimps captured in the bottom trawl. Pelagic shrimp fed opportunistically on a variety of zooplankters, using copepods as a staple food. Stomachs of shrimp from the bottom trawl contained chitinous debris, sand grains, and small amounts of benthic organisms. The occurrence of daily vertical feeding migrations results in the unavailability of a variable proportion of the total shrimp biomass to bottom trawls.

La distribution verticale et le régime alimentaire de la crevette (*Pandalus montagui*) furent étudiés au moyen d'un échantillonneur à plancton à étages multiples (BIONESS) et comparées avec les captures au fond avec un chalut. La crevette effectue d'importantes migrations verticales nocturnes associées à une activité intense d'alimentation pélagique. La représentation des sexes, la distribution des fréquences de taille et le régime alimentaire des crevettes capturées dans la colonne d'eau différaient clairement de ceux des captures du chalut. Les migrateurs pélagiques étaient principalement (75 %) des mâles, prolongeant leur séjour planktonique en matinée, tandis que les femelles ovigères (12 %) et non ovigères (13 %) retournaient au fond à l'aube. Dans le chalut, la représentation des mâles (43 %) et des femelles ovigères (45 %) différait, mais fluctuait aussi selon le cycle diurne. L'estomac des crevettes du BIONESS était mieux rempli et leur contenu en meilleure condition que celui des crevettes capturées au fond dans le chalut. Les crevettes pélagiques s'alimentaient de manière opportuniste d'une variété d'organismes zooplanktoniques, utilisant les copépodes comme aliment de base. L'estomac des crevettes dans le chalut comprenait des débris chitineux, des grains de sable et de faibles quantités d'organismes benthiques. La migration verticale journalière des crevettes pour leur alimentation soustrait une proportion variable de la biomasse totale à la capture dans les chaluts de fond.

Received February 15, 1991
Accepted October 4, 1991
(JA902)

Reçu le 15 février 1991
Accepté le 4 octobre 1991

Pandalid shrimp (*Pandalus* spp.) were originally believed to be primarily benthic feeders (Hjort and Ruud 1938; Mistakidis 1957; Allen 1963). The diet of *Pandalus borealis* at a variety of locations included benthic crustaceans, polychaetes, bottom foraminiferans, radiolarians, phytobenthos, excrement pellets, and sand (Squires 1965; Neelakantan 1975). Other studies documented the occurrence of pelagic prey (Horsted and Smidt 1956; Allen 1959; Squires 1965) or of a mixture of pelagic and benthic prey items reflecting local species composition (Mistakidis 1957; Allen 1963). These observations suggested that the spectrum of food organisms available to *P. borealis* determined the composition of its diet and that the availability of prey items was related to the daily vertical migrations of shrimp (Horsted and Smidt 1956; Berenboim 1981; Wienberg 1981).

Shrimp vertical migrations were used to partly explain the diel fluctuations of catch rates and sex/size composition observed in bottom trawl captures (Carlsson et al. 1978; Fréchette et al. 1984; Shumway et al. 1985). The low catch rates observed at night were explained by shrimp movement off the bottom. Also, an increase in the proportion of ovigerous females on the bottom was observed at night, explained by the better swimming ability and more extensive vertical migrations of smaller males and nonovigerous females. The linkage between planktonic feeding activity and vertical migration was clearly established when the origin of prey items in the shrimp diet was found to vary with the time of day and the developmental stage of the shrimp (Wienberg 1981). Barr (1970) suggested that the consumption of planktonic prey would be greater by juveniles and males than by females, since the latter were thought not to migrate as extensively as the former. Male shrimp were also found to feed on plankton in the pelagic zone more actively than females (Wienberg 1981). However, Allen (1963) found that maturity had little obvious effect on feeding, with the possible exception of females bearing eggs. The extent of planktonic feeding activity is related to the extent of vertical migrations, as determined by the swimming ability of animals of different size/sex (Allen 1963; Barr 1970; Wienberg 1981).

---

[1] Present address: Department of Fisheries and Oceans, Science Branch, Halifax Fisheries Research Laboratory, P.O. Box 550, Halifax, N.S. B3J 2S7, Canada.

This study integrates the diel vertical migration and feeding activity of shrimp by comparing the biological characteristics and diet of animals captured in the water column and near the bottom. It is part of a wider program investigating the distribution of *Pandalus montagui* by acoustic echo-integration and bottom trawling off Resolution Island (Parsons et al. 1990; Crawford et al. 1992). Since 1979, high concentrations of this species have been exploited commercially in eastern Hudson Strait, which is characterized by high tidal amplitudes (Canadian Hydrographic Service 1988) and swift currents (Canadian Hydrographic Service 1983). It was expected that the occurrence of high shrimp densities in such a dynamic environment would facilitate the study of their vertical migrations and of their interaction with feeding activity.

Material and Methods

Sampling was carried out between August 22 and September 2, 1988, west of Resolution Island (eastern Hudson Strait) (Fig. 1). The survey grounds consisted of a 800-km^2 coffin-shaped pentagon which defined the area where shrimp catches of previous years (from both research and commercial vessels) were concentrated (Hudon 1990). The vertical distribution of shrimp was studied over the diel cycle using a 1-m^2 aperture, multiple-net zooplankton sampler with a remote control net opening/closing device (BIONESS; Sameoto et al. 1980).

BIONESS sampling was conducted every 2 h for three series of 13, 27, and 27 h, respectively, over a period of 1 wk. Each BIONESS tow was made at 3 m·s^{-1}, using nine nets. The descending part of each BIONESS set was made with all nets closed. The first net was opened about 10 m (mean = 12.5 m) above the bottom (mean = 282 m) and sampled the next upper 25-m layer. The next six nets were opened sequentially at each 25-m interval, and the last two nets sampled a 50-m stratum each, to the surface (Table 1). Each net was open for about 3 min, filtering about 450 m^3 of water. Filtering efficiency, monitored during the sampling process and calculated as the ratio of values from internal and external flowmeters mounted on the BIONESS, was always over 65%. A total of 34 tows were made, resulting in the collection of 293 samples out of a maximum possible of 306. Physical conditions during each tow (depth, temperature, salinity, towing speed, and internal and external flowmeter values) were simultaneously transmitted to the surface and recorded on a microcomputer. A detailed analysis of shrimp and other macrozooplankters' vertical migrations with respect to physical factors (temperature, salinity, density, and light intensity) is currently under way (C. Hudon et al., in prep.).

The nets used in the BIONESS were of 500- and 333-μm mesh. Zooplankton samples were preserved in 10% formalin, sorted into 11 major taxonomical groups, enumerated, and weighed (0.01 g) after removing the excess water by straining through a <333-μm nitex sieve. A composite species list was derived from all samples. Concentration of each group of zooplankters was calculated in milligrams per cubic metre for each net sample. Shrimp oblique carapace length, defined as the distance from the posterior margin of the orbit to the posterodorsal margin of the carapace (Rasmussen 1953), was measured to the nearest 0.1 mm. *Pandalus montagui* is a protandric hermaphrodite. Males, transitionals, and females were separated by examining the characteristics of the endopod of the first pleopod (Rasmussen 1953). Transitional shrimp represented a very small proportion (<2%) of all captures and were included with nonovigerous females for calculations. Egg-bearing (ovigerous) females were separated from those without eggs.

Data on the diel cycle of shrimp catches and composition were obtained from two series of trawl sets made in the coffin-shaped area (Fig. 1) in 1988 (n = 20 tows) and 1982 (n = 15 tows). In order to minimize the variability due to depth and location, a subset of six tows from 1988 (indicated on Fig. 1) were used for the comparison of size structure of shrimp captured in the BIONESS.

Analyses of stomach contents and electivity (''preference'' index) were carried out on all the shrimp captured in the second BIONESS series (13 tows over 27 h), which captured the highest number (n = 365) of shrimp. Shrimp (n = 107) from two of the 1988 trawl sets (conducted at 15:54 and 23:00) were used for stomach contents analysis to compare with shrimp captured in the BIONESS while accounting for a possible day–night variation of stomach content. The same procedure of stomach content analysis was used for shrimp captured in the BIONESS and the trawl samples: stomach fullness was ranked from 0 (empty) to 5 (full); the state of preservation of the contents was evaluated between 0 (unidentifiable digested matter) and 5 (intact material). Food items were sorted and identified to the highest possible taxonomic precision. The proportion of each major food item was evaluated from 0 to 5, on the basis of its abundance in the stomach. The sum of the proportions of each food item in each stomach equalled 5, regardless of stomach fullness.

A diel cycle of stomach fullness (ranked as empty, some food, or full) was obtained from samples (n = 5440 shrimps) from 13 of the 1982 diel series of trawl tows. Both 1988 and 1982 trawl samples were taken from standard, 30-min survey sets using the Sputnik 1600 shrimp trawl (40-mm mesh size) lined in the codend with 13-mm mesh. The trawl's headrope extended 7 m above the bottom whereas the deepest BIONESS net (No. 1) sampled at an average distance of 24 m (range 12–37 m) above the bottom.

Statistical Analyses

The catch efficiency of shrimp in the BIONESS was calculated using the equation (Clutter and Anraku 1968)

$$(1)\quad 1 - 1/\pi R^2\,[a\,(R^2 - a^2/4)^{1/2} + 2R^2 \sin^{-1} a/2R]$$

where R represents the net radius and a is the distance a shrimp can move between the time of response and the moment at which the net reaches its plane. Since the mouth of the BIONESS is square (1 × 1 m), we used the conservative R value of 0.5 m, which represents the minimal escape distance at a right angle from the BIONESS trajectory. For the calculation of a, we assumed that shrimp reach a peak burst speed of at least 1 m·s^{-1} and that they perceive the approaching net (mov-

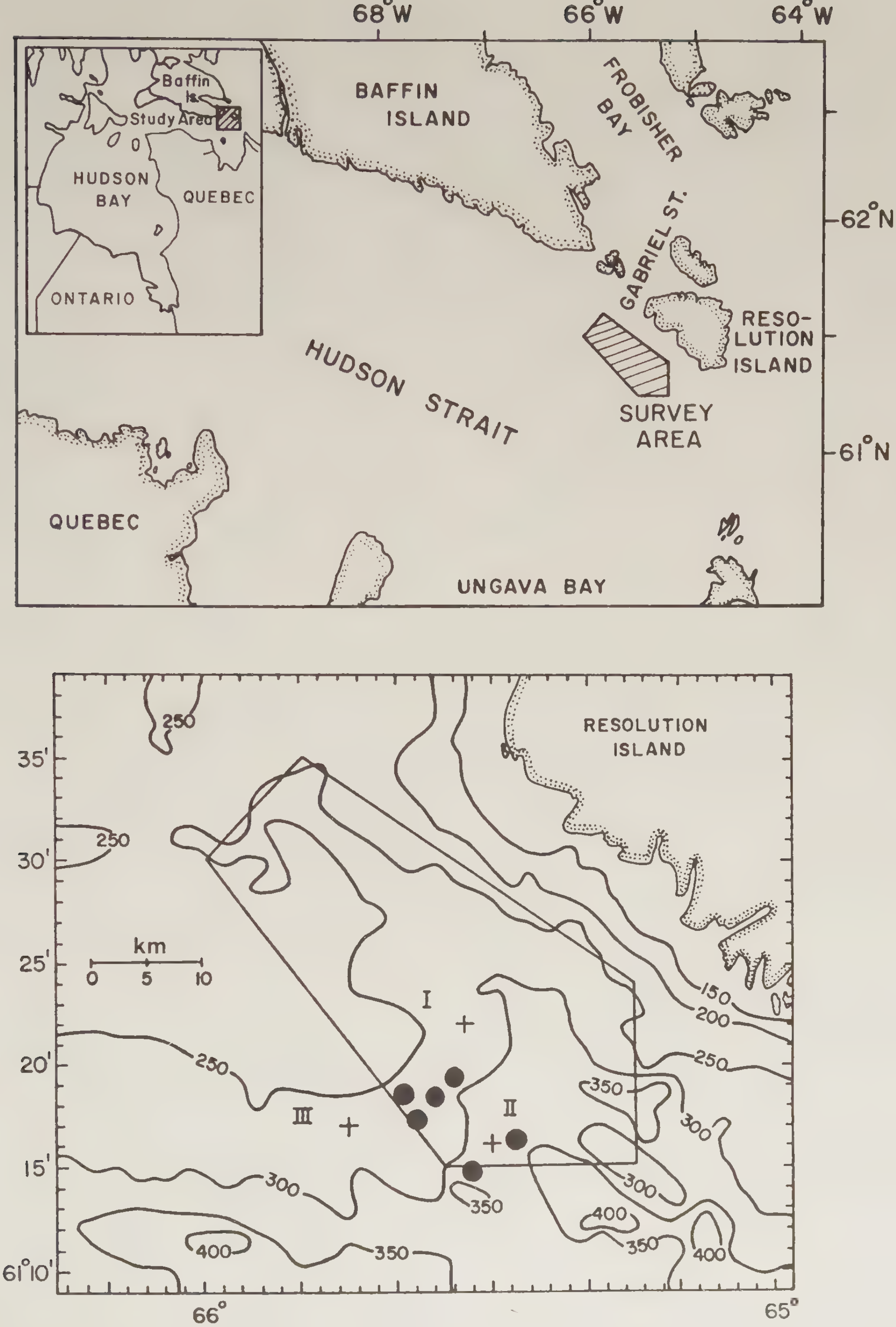

68°W
66°W
64°W
62°N
61°N
Baffin Is.
Study Area
HUDSON BAY
QUEBEC
ONTARIO
BAFFIN ISLAND
FROBISHER BAY
GABRIEL ST.
RESOLUTION ISLAND
HUDSON STRAIT
SURVEY AREA
QUEBEC
UNGAVA BAY
RESOLUTION ISLAND
35'
30'
25'
20'
15'
61°10'
66°
65°
km
0
5
10
250
250
250
150
200
250
350
300
300
300
350
400
350
350
400
400
I
II
III

FIG. 1. Location of the study area, west of Resolution Island, in eastern Hudson Strait. The hatched coffin-shaped area indicates the location where large catches of shrimp were made in previous years and where the acoustic survey was conducted and the 1988 and 1982 bottom trawl samples taken. A composite shrimp sample from a subset of six bottom trawl sets (1988) (black circles) was used for comparison of size structure, two of which were analyzed for shrimp diet on the bottom. Location of BIONESS series I, II, and III are indicated with a cross. Shrimp from BIONESS series II (13 sets) were used for stomach content identification.

ing at 3 m·s^{-1}) a minimum of 1 m before it reaches their plane (see fig. 3 in Clutter and Anraku 1968). Those values allowed us to calculate the maximum possible value of BIONESS catch efficiency for shrimp.

The difference of size distribution between shrimp captured in the BIONESS and in the bottom trawl was tested using a chi-square test.

Samples from the three BIONESS series were grouped according to four time intervals (sets conducted at 00:00–6:00, 6:00–12:00, 12:00–18:00, and 18:00–24:00) and three depth

TABLE 1. Proportion of each sexual group observed in each net of the BIONESS. For each net, the average depth from the surface and above the bottom is indicated in metres.

	BIONESS net No.								
	9	8	7	6	5	4	3	2	1
Depth from surface	41.2	84.1	114.4	139	163.6	188.6	212.5	235.5	258
Distance to bottom	240.8	197.9	167.6	143	118.4	93.4	69.5	46.5	24
Number of shrimp	16	60	23	92	62	63	90	79	87
% males	100	75.4	68.8	71.6	80.0	72.6	71.7	72.0	78.2
% females	0	6.2	15.6	17.0	9.2	16.1	15.2	9.3	19.2
% ovigerous females	0	18.4	15.6	11.4	10.8	11.3	13.1	18.7	2.6

strata measured from the surface (0–125, 126–200, and >201 m) roughly coinciding to nets 7–9 (surface), 4–6 (midwater), and 1–3 (bottom). The diel variations in shrimp concentrations, individual shrimp weight, and percentage of ovigerous females captured at different depths in the BIONESS were analyzed using two-way ANOVAs (time interval, depth strata, and time × depth). The yearly and diel variations in shrimp catches and composition in the 1988 and 1982 bottom trawl samples were tested with two-way ANOVAs (year, time interval, and year × time). Trawl catch data were $\log_{10}$ transformed to homogenize the variance among groups of samples.

The occurrence of net feeding by shrimp was tested using ANOVA by comparing the degree of stomach fullness and of preservation of the stomach contents between shrimp captured in successive nets for four BIONESS sets in which shrimp were captured in all nets. It was hypothesized that, if shrimp fed in the net, their stomachs would be fuller and in a better preservation state in the nets opened first (bottom nets) than in nets opened last (surface nets).

The preference of shrimp for specific categories of food items was tested using an electivity index based on the difference in the abundance ranking of available zooplankters (R_{zoo}) relative to the ranking of prey items in the stomachs (R_{gut}) (Johnson 1980). For this, the concentration of each zooplankter group captured in each net (milligrams per cubic metre) and the food items found in the stomach of each shrimp (abundance from 0 to 5) caught in that same net were ranked in decreasing order. Electivity was evaluated from the difference in rank ($R_{zoo} - R_{gut}$) for each category of organism. The shape of the frequency distribution of electivity values for a large number of samples (shrimp stomachs) represents the selection curve for or against each prey type.

Results

Daily Cycle of Shrimp Vertical Migrations

Analysis of BIONESS samples revealed the occurrence of a diel vertical migration cycle of shrimp off the bottom. The bulk of shrimp captures were made during the evening and at night, at which time they were found throughout the water column. Smaller concentrations of shrimp were present in the water column in the morning whereas daytime shrimp captures were restricted to bottom nets (Table 2). Significantly higher shrimp concentrations were captured during hours of darkness (evening and night) than in daylight hours (morning and day) (ANOVA on concentrations in weight: $F = 15.66$, 3 df, $P = 0.0001$; in numbers: $F = 15.92$, $P = 0.0001$). The onset of vertical movements roughly coincided with diminishing light intensity, but the timing of peak vertical displacement varied between BIONESS series. Shrimp distribution in the water column was very patchy, with high concentrations sometimes alternating with empty nets. This observation was confirmed by acoustic data, showing the occasional occurrence of dense shrimp clouds oscillating in the midwater area. As a result, no significant difference in shrimp concentration was observed among depth strata (ANOVA on concentration in weight: $F = 1.15$, 2 df, $P = 0.3168$; in numbers: $F = 1.33$, $P = 0.2655$) (Table 2). The interaction term between time interval and depth was not significant.

Bottom trawl catches were highly variable (Table 2) even after transformation, resulting in the absence of significant differences between years and time intervals (ANOVA, year, time, year × time: $F = 1.85$, 7 df, $P = 0.1190$). For each year, highest captures were made during different time intervals. In 1988, an average 1122 kg of shrimp was caught per tow in daytime whereas in 1982 the maximum average catch of 626 $kg \cdot tow^{-1}$ occurred at night.

The average weight of individual shrimps (Table 3) captured in the BIONESS was examined during the same time intervals to determine if catch composition varied with time and depth. Weight rather than carapace length was selected for its capability to simultaneously account for size and reproductive status of shrimp (ovigerous females). Shrimp captured in the evening (18:00–24:00, group A) were significantly heavier ($F = 4.48$, 3 df, $P = 0.0040$) than those captured in the morning (06:00–12:00, group C) (Table 3). The effect of depth strata ($F = 0.29$, 2 df, $P = 0.7476$) and the interaction between time and depth ($F = 0.48$, 5 df, $P = 0.7923$) were not significant. This indicates that large shrimp made distinct pelagic migrations into the water column at night whereas smaller shrimp (predominantly males) tended to remain in the water column (albeit in low densities) during daytime. The periods during which the large shrimp progressively migrate up (12:00–18:00) and down (00:00–06:00) corresponded to the mixing of large and small shrimp and result in a median group (B, Table 3) of overlapping weight.

In order to investigate further the temporal differences in shrimp individual weight reported above, the proportion of ovigerous females captured per net was calculated for each time and depth interval (Table 4). A similar model ANOVA (time, depth, and time × depth) yielded a significantly higher proportion of ovigerous females during hours of darkness (18:00–06:00) than during daylight (06:00–18:00) ($F = 6.28$, 3 df, $P = 0.0004$). These results indicate that the increased proportion of ovigerous females captured in the water column at night (Table 4) accounted for the higher individual shrimp

TABLE 2. Average shrimp concentrations per 1000 m^3 of water expressed in weight (g) and average number of shrimp in BIONESS samples made over four time intervals and three depth strata. The number of shrimp and nets sampled in each cell can be found in Tables 3 and 4, respectively. Corresponding shrimp captures (kg 0.5-h standard tow) in bottom trawl samples (mean, SD, n) in 1988 and 1982 are indicated below. BIONESS captures during the evening and at night were significantly higher than during the morning and the day. Trawl captures did not show any significant difference among time intervals due to high catch variability and small set number.

	Night (00:00–06:00)	Morning (06:00–12:00)	Day (12:00–18:00)	Evening (18:00–24:00)
Depth strata	Weight and no. of shrimp	Weight and no. of shrimp	Weight and no. of shrimp	Weight and no. of shrimp
0–125 m	48.6	3.1	0	20.0
(nets 7–9)	11.0	0.8	0	4.0
126–200 m	41.1	3.2	0.2	53.9
(nets 4–6)	8.8	0.9	0.1	11.7
>201 m	42.7	16.1	23.6	21.4
(nets 1–3)	9.3	4.0	5.5	4.5
Overall	43.9	7.6	8.7	33.5
BIONESS	9.7	1.9	2.0	7.1
Trawl				
1988	137.73	408.23	1122.45	430.43
	151.45, 7	585.99, 5	887.96, 4	345.19, 4
1982	626.14	116.57	412.50	266.83
	110.43, 5	0, 1	172.29, 5	79.49, 4

TABLE 3. Average individual wet weight (g), standard deviation (SD), and number of shrimp (n) captured using the BIONESS over four time intervals and three depth strata. Shrimp captured during the evening and at night were significantly heavier than those captured during the day and morning. Significantly different individual weight values (P = 0.004) among time intervals are indicated by different letters (groups). Weight did not vary significantly among depth strata, and the interaction term was not significant.

	Night (00:00–06:00)	Morning (06:00–12:00)	Day (12:00–18:00)	Evening (18:00–24:00)
Depth strata	Weight (SD, n)	Weight (SD, n)	Weight (SD, n)	Weight (SD, n)
0–125 m	4.77	3.52	—	4.99
(nets 7–9)	(1.87, 81)	(1.97, 9)	0	(1.41, 46)
126–200 m	4.40	3.85	3.12	4.69
(nets 4–6)	(1.41, 65)	(1.42, 15)	(0, 1)	1.84, 125)
>201 m	4.35	4.07	4.15	4.82
(nets 1–3)	(1.41, 69)	(1.58, 54)	(1.42, 77)	(1.82, 30)
Overall weight	4.52	3.96	4.14	4.78
Groups	AB	C	BC	A

weight recorded during the same period (Table 3). With depth, ovigerous females represented a smaller proportion of shrimps captured in midwater samples (F = 4.03, 2 df, P = 0.0187). The differences observed among depth strata suggest that ovigerous females occurred sporadically in the water column, rather than as a systematic progression of individuals from the bottom upwards. The interaction time (time × depth) was not significant (F = 0.31, 5 df, P = 0.9308).

The sporadic occurrence of ovigerous females in the water column was further supported by the much higher proportion they represented in bottom trawl captures (Table 4) (overall 1988 trawl samples average = 45.5%). Similar to what was observed in the BIONESS, highest proportions of ovigerous females in both trawl series were captured in hours of darkness (18:00–06:00), although only significantly so in 1982 (F = 4.83, 3 df, P = 0.0285). A regular progression in catch composition was observed over the diel cycle during the series of bottom trawl sets made in 1982, which comprised a smaller proportion during daylight (05:00–17:00) (Fig. 2). The curves for males and ovigerous females showed opposite trends, while the proportion of nonovigerous females remained relatively stable in bottom trawl samples over the entire diel cycle.

Biological Characteristics of Pelagic versus Benthic Shrimp Captures

Once the diel fluctuations of catch abundance and composition in the BIONESS and in the trawl are taken into account,

Table 4. Average percentage of ovigerous females per net, standard deviation (SD), and number of nets (n) sampled by the BIONESS over four time intervals and three depth strata. Corresponding values of the percentage of ovigerous females in trawl catches (mean, SD, n) in 1988 and 1982 are indicated below. In the BIONESS and in the 1982 trawl samples, the percentage of ovigerous females captured during the evening and at night was significantly higher than during the morning and the day. Percentage of ovigerous females in the midwater depth stratum was significantly lower than in the other strata. The interaction term was not significant.

Depth strata	Night (00:00–06:00) % (SD, n)	Morning (06:00–12:00) % (SD, n)	Day (12:00–18:00) % (SD, n)	Evening (18:00–24:00) % (SD, n)
0–125 m (nets 7–9)	10.7 (25.8, 15)	1.1 (6.2, 29)	0 (0, 22)	9.1 (19.8, 23)
126–200 m (nets 4–6)	4.6 (10.2, 18)	0 (0, 39)	0 (0, 27)	8.7 (15.6, 24)
>201 m (nets 1–3)	10.8 (22.2, 17)	4.3 (12.5, 36)	7.7 (26.2, 28)	15.8 (26.9, 15)
Overall BIONESS	8.5	1.8	2.8	10.6
Trawl				
1988	38.4 (23.6, 7)	26.2 (10.5, 5)	21.8 (3.9, 4)	39.5 (23.8, 4)
1982	22.2 (6.5, 5)	4.0 (0, 1)	18.5 (3.9, 5)	33.7 (11.6, 4)

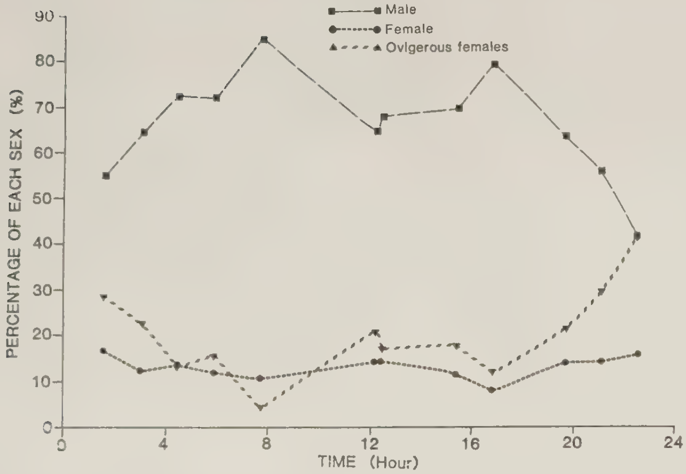


Fig. 2. Diel variations of the proportion of each sexual group in a bottom trawl over a 24-h diel cycle in the Resolution Island area in 1982.

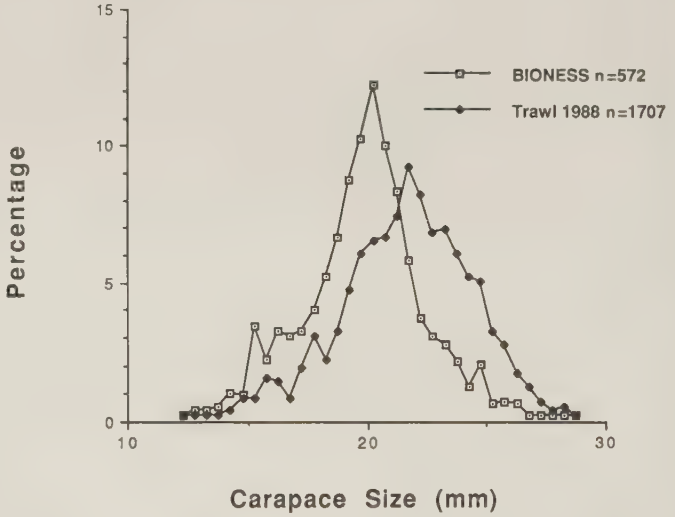


Fig. 3. Size frequency distribution of shrimp captured using the BIONESS and the 1988 composite trawl sample from the Resolution Island area.

major differences remain between the overall composition of each gear's captures. In the BIONESS, males represented the bulk (74.6%) of the catch, with roughly equivalent proportions of nonovigerous (13.3%) and ovigerous females (12.1%). The representation of each sex did not vary with net, except in the one nearest the surface, where only males were found (Table 1). In contrast, 1988 trawl catches comprised equivalent proportions of males (43.4%) and ovigerous females (45.5%), with a small representation of nonovigerous females (11.1%). The difference in proportion of sexes was also perceptible in the smaller overall mean size for the shrimp sampled in the water column (mean carapace length (CL) = 19.55 mm) than in the bottom trawl (mean CL = 21.38 mm). The size frequency distribution of shrimp captured in the water column using the BIONESS differed (χ^2 = 254.05, 32 df, $P < 0.001$) from that of shrimp captured on the bottom with the trawl (Fig. 3). It must be noted that gear selectivity alone could result in the observed differences in shrimp size structure, since they act in opposite directions: large shrimp could successfully avoid the BIONESS but could be more effectively retained by the large mesh used in the bottom trawl.

Calculation of the catch efficiency coefficient using Clutter and Anraku's (1968) equation yielded a negative efficiency value ($C = -11.298$), suggesting that our shrimp captures were above the expected performance of the net.

Abundance and Vertical Distribution of Potential Food Items

Forty-nine species belonging to 13 groups were identified in the zooplankton samples and in the trawl (Table 5). Ctenophora

TABLE 5. Organisms captured in the BIONESS and in the bottom trawl. Highlighted species were the most common in each group. Where appropriate, the life stage of the organism is indicated: L, larva; J, juvenile; A, adult.

Family	Genus	Species	BIONESS	Trawl
Cnidaria	***Aglantha***	***digitale* (O.F. Muller)**	×	
	Atolla	spp.		
Ctenophora	***Beroe***	***cucumis* Fabricius?**	×	
Chaetognatha	*Sagitta*	*elegans* Verrill	×	
	Sagitta	*maxima* (Connant)	×	
	Eukrohnia	***hamata* (Mobius)**	×	
Polychaeta	*Tomopteris*	*septentrionalis*	×	
	Autolytus	spp.	×	
Ostracoda	*Conchoecia*	*elegans* Sars	×	
	Conchoecia	*borealis*	×	
Copepoda	***Calanus***	***glacialis* Jaschnov**	×	
	Calanus	***finmarchicus* (Gunnerus)**	×	
	Calanus	*hyperboreus* Krøyer	×	
	Metridia	longa (Libbock)	×	
	Bradyidius	*similis* (G.O. Sars)	×	
	Pseudocalanus	*minutus* (Krøyer)	×	
	Microcalanus	*pusillus* G.O. Sars	×	
	Scolecithricella	*minor* (Brady)	×	
	Euchaeta	*norvegica* Boeck	×	
	Oithona	*similis* Claus	×	
	Heterorhabdus	*norvegicus* (Boeck)	×	
Mysidacea	*Boreomysis*	*arctica* (Krøyer)	×	
	Mysis	***polaris* Holmquist**	×	
	Meterythrops	***robusta* S.I. Smith**	×	
Amphipoda	***Themisto***	***compressa* Goes**	×	
	Themisto	*libellula* (Lichtenstein)	×	
	Themisto	*abyssorum* Boeck	×	
	Hyperia	*galba* (Montagu)	×	
	Onisimus	*litoralis* (Krøyer)	×	
	Gammarus	*setosus* Dementieva	×	
	Halirages	*fulvocinctus* (M. Sars)	×	
Euphausiacea	*Meganyctiphanes*	*norvegica* (M. Sars)	×	×
	Thysanoessa	***inermis* (Krøyer)**	×	×
	Thysanoessa	*longicaudata* (Krøyer)	×	
	Thysanoessa	*raschi* (M. Sars)	×	
Decapoda	***Pandalus***	***montagui* (Krøyer)**	×	×
	Pandalus	*borealis* (Krøyer)	×	×
Pteropoda	***Clione***	***limacina* (Phipps)**	×	
	Spiratella	***helicina* (Phipps)**	×	
Cephalopoda	*Gonatus*	*fabricii* (Lichtenstein)?	J	A
Pisces	*Triglops*	*nybelini* Jensen	J, A	A
	Myoxocephalus	*scorpius* Linne	L	A
	Sebastes	*mentella* (Linne)	J	A
	Liparis	*fabricii* Krøyer	L, J, A	A
	Hippoglossoides	*platessoides* (Fabricius)	L	J, A
	Triglops	*murrayi* Gunther	J	A
	Reinhardtius	*hippoglossoides* (Walbum)	L	J, A
	Bathylagus	*euryops* Goode & Bean	L	A
	Liparis	*tunicatus* Reinhardt	L	A
	Gadus	spp.	L	A
	Gonostomatidae		L	A
	Myctophidae		L	A

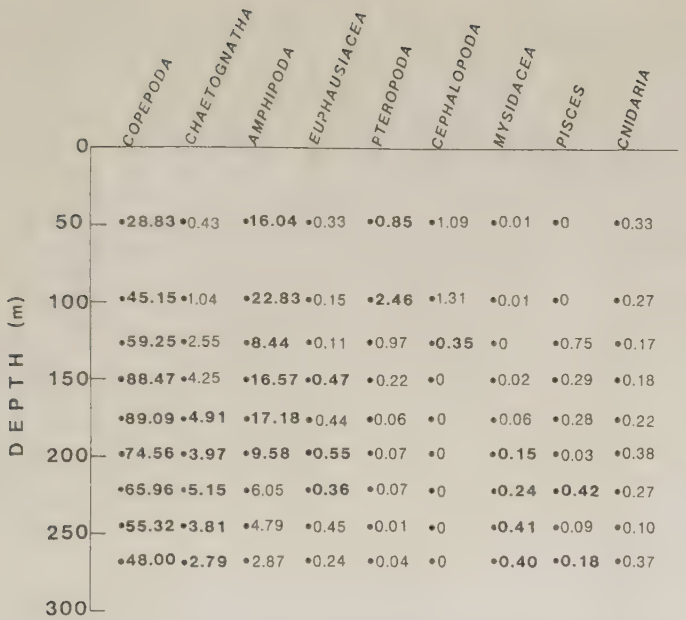


FIG. 4. Average diel concentration of the major groups of prey organisms (mg·m^{-3}) at each depth sampled by the BIONESS. The bold values correspond to the depths at which each group was consumed by shrimp.

were difficult to identify and enumerate due to poor preservation and were not considered in the analysis. Copepods (11 species) and pisces (12 species/families) were the most diversified groups.

Copepods and chaetognaths were common over the entire water column but were in highest concentration at middepth (125–200 m) (Fig. 4). Amphipods (to 200 m), pteropods (to 100 m), and cephalopods (to 125 m) were prevalent in the surface waters whereas mysids were most concentrated near the bottom (275–350 m). Euphausiids, pisces, and cnidarians occurred in small concentrations throughout the water column.

Comparison of Diet in BIONESS versus Trawl

Stomach fullness and the state of preservation of contents covaried differently depending on sampling gear (Table 6). In the BIONESS, shrimp stomachs were generally full of well-preserved or intact material, without difference between sex or size. In the trawl, shrimp stomachs contained variable amounts of mostly digested material, also regardless of sex or size.

Comparison of stomach fullness and preservation of contents for four BIONESS sets where shrimp occurred throughout the water column indicated that feeding took place in the two bottom nets. Stomach fullness was marginally higher ($F = 1.88$, 8 df, $P = 0.065$) and stomach contents were significantly better preserved ($F = 3.31$, 8 df, $P = 0.002$) for shrimp captured in bottom nets (nets 1 and 2) than in nets opened near the surface at the end of the set (nets 8 and 9).

Over the diel cycle, mean stomach fullness ($F = 1.15$, 3 df, $P = 0.328$) and preservation state ($F = 2.00$, 3 df, $P = 0.114$) did not vary in the BIONESS. The interaction term between depth and time intervals was never significant. In the series of bottom trawl samples obtained in 1982, no diel variation of mean index of stomach fullness could be detected, possibly as a result of the use of only three categories (empty, some food, and full).

The prey species found in the stomachs also differed between methods of collection (Table 7). Copepods, chaetognaths,

TABLE 6. Contingency tables of the percentage representation of ranks of stomach fullness and the preservation state of contents for shrimp captured in BIONESS series II (top, $n = 365$) and in the trawl (bottom, $n = 107$). The highest values are highlighted.

Preservation state		Stomach fullness Empty 0	1	2	3	4	Full 5	Sum
				BIONESS				
Digested	0	5.5	0.0	0.0	0.0	0.3	0.0	5.8
	1	0.0	5.5	0.3	0.8	0.3	0.3	7.1
	2	0.0	1.1	1.1	4.1	0.5	0.0	4.1
	3	0.0	0.8	2.7	4.9	**8.8**	4.9	22.2
	4	0.0	0.5	2.2	6.6	**12.9**	**14.2**	36.4
Intact	5	0.0	0.0	0.3	3.8	5.5	**14.8**	24.4
Sum		5.5	7.9	6.6	17.5	28.2	34.2	100.0
				Trawl				
Digested	0	**26.2**	0.0	0.0	0.0	0.0	0.0	26.2
	1	0.0	**29.9**	**9.3**	**7.5**	**11.2**	**5.6**	63.6
	2	0.0	0.9	1.9	1.9	0.9	0.9	6.5
	3	0.0	0.9	0.9	0.0	0.0	1.9	3.7
	4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Intact	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sum		26.2	31.8	12.1	9.3	12.1	8.4	100.0

TABLE 7. Frequency of occurrence (percentage) of each type of prey observed in the stomachs of shrimp captured in BIONESS series II ($n = 365$) and in the trawl ($n = 107$).

		BIONESS (%)	Trawl (%)
Pelagic prey	Copepoda	88.3	0.0
	Chaetognatha	50.7	0.0
	Hyperida	37.7	0.0
	Ostracoda	33.7	0.0
	Euphausiacea	8.2	0.0
	Pteropoda	7.7	1.9
	Hydrozoa	7.1	5.6
	Cephalopoda	4.9	0.0
	Mysidacea	4.9	0.0
Benthic prey	Foraminifera	2.2	22.4
	Pelecypoda	1.9	1.1
	Ascidiacea	1.6	0.9
	Polychaeta	1.4	15.9
	Mollusca	0.8	0.0
	Gastropoda	0.8	0.0
	Pisces	0.8	1.9
	Cnidaria	0.5	0.0
	Ophiuroida	0.5	3.7
	Gammaridea	0.3	5.7
	Decapoda	0.3	0.0
	Algae	0.0	1.9
	Crustacea	0.0	0.9
Digested material	Organic matter	41.9	68.2
	Sand	13.4	69.2
	Tissue	8.2	0.0
	Cuticle	0.3	27.0
Empty stomachs		5.2	26.0

hyperiid amphipods, and other planktonic organisms were the principal prey of shrimp collected in the BIONESS. Foraminiferans, polychaetes, amphipods, and other benthic prey were most frequent in the stomachs of shrimp captured with the trawl. Also, unidentifiable organic matter, sand, and cuticle fragments were more frequent in the trawl samples.

Pelagic prey were consumed with different intensity with depth (Fig. 4, bold characters), showing that only copepods were frequently consumed at all depths. Up to 59 copepods were found in a single shrimp stomach. Although copepods represented the basic staple food for shrimp, the frequency of secondary prey (hyperiid amphipods, chaetognaths, euphausiids, mysids, and pteropods) shifted with depth, corresponding to the relative prey availability. In deep layers, shrimp consumed mysids and chaetognaths. In midwater, euphausiids were included in the diet whereas in near-surface waters, hyperiid amphipods and pteropods became gradually more prevalent.

In the BIONESS samples, the depth of shrimp capture was not the only factor explaining the importance of planktonic or benthic prey. Pelagic prey were consumed by animals at all depths whereas remains of benthic prey could be found in the stomachs of shrimp captured up to 200 m off the bottom.

Comparison of Food Ingested versus Its Availability

A frequency histogram of the electivity index for each prey type (Fig. 5) indicated differential consumption of the various prey items. Positive values were observed if a prey had a lower abundance rank in the stomach than in the environment and resulted in a frequency distribution skewed to the right, as was the case for hyperiid amphipods (mean = 1.75, SD = 2.35, *n* = 327) and euphausiids (mean = 0.89, SD = 1.64). Zero or near-zero index values mean that the prey was eaten in proportion to its abundance rank in the plankton. The narrow distribution about zero of the index for copepods (−0.37, 1.52) supports its use as staple food whereas the normal distribution for cnidarians (0.27, 1.48) suggests that its consumption was opportunistic or accidental. Negative values of the index were obtained when a prey (pteropods, cephalopods, and pisces) was more important in the stomach than in the zooplankton, indicating a preference. However, the very low concentration of the latter two groups in the zooplankton might have artificially increased their preference value. All means were significantly different from zero, except for chaetognaths (−0.15, 2.28) and mysids (−0.8, 2.25).

A similar pattern was obtained when the representation of each prey group was calculated as a percentage of the total biomass. Copepods represented the bulk of shrimp diet (60.3% of prey) as well as in the zooplankton (74.2% of biomass). Hyperiid amphipods (10.6% prey versus 9.5% biomass), chaetognaths (17.3% prey versus 4.2% biomass), pteropods (2.4% prey versus 0.5% biomass), and other zooplankters followed a decreasing order of importance.

Discussion

Although the nighttime migration of shrimp in the water column was previously inferred from temporal fluctuations of bottom trawl catches, studies based on direct measurements of shrimp as they migrate into the water column were rarely carried out (Barr 1970). Our results showed that shrimp abundance and sex composition in the water column varied markedly over the diel cycle, demonstating the relationship between vertical migrations and shrimp feeding activity, resulting in temporal changes in bottom trawl captures and sex composition.

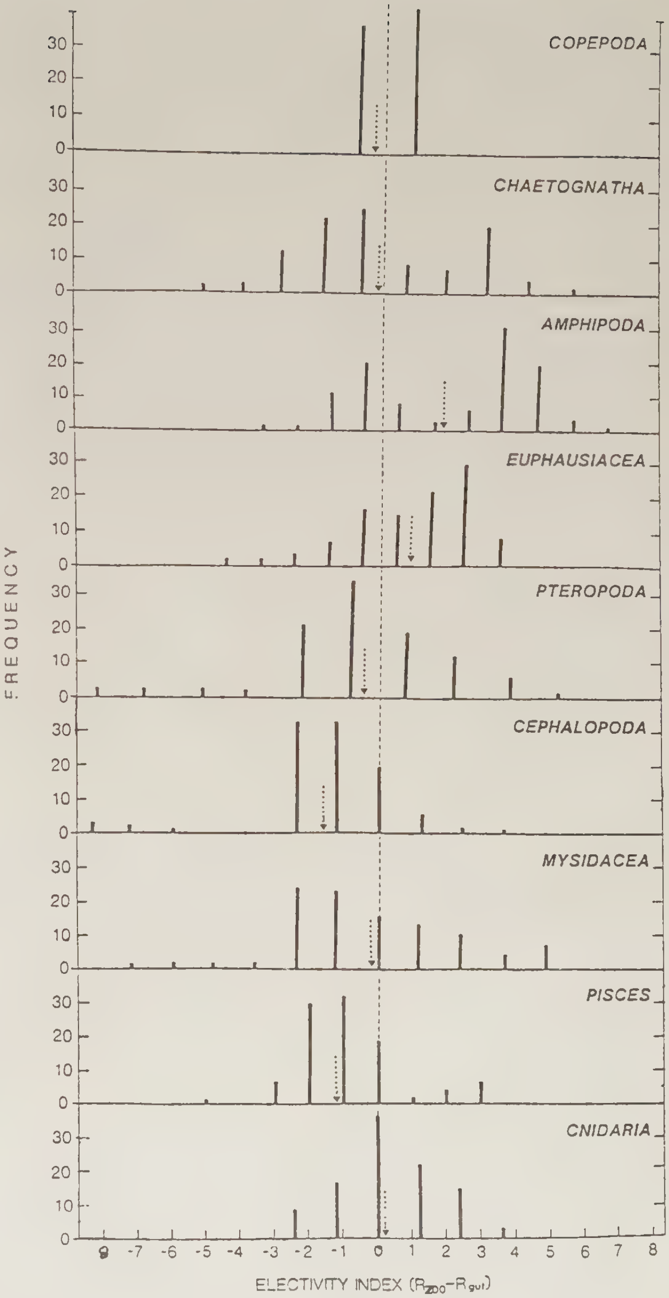


FIG. 5. Frequency distribution of the electivity index for the most common prey of shrimp captured in BIONESS series II. Individual dotted arrows indicate the average electivity value for each group. The vertical broken line refers to the baseline value (indifference). Negative electivity values indicate that the prey item has a higher rank of abundance in the stomach than in the zooplankton (preference) whereas positive values indicate the opposite (avoidance).

Shrimp Diel Vertical Migration Cycle

Our results showed that shrimp made distinct pelagic migrations in the water column during the evening and the night and that most of them returned to the bottom during the morning and daytime (Table 2). Shrimp captures in the bottom trawl tended to be higher during daylight hours but failed to show a significant diel trend due to their high variability. In addition to the diel fluctuation in total catch, differential migrations occurred with different shrimp size (sexual groups). The average individual weight of shrimp occurring in the water column in the hours of darkness (evening and night) was significantly larger than in daylight hours (Table 3). This was due to the presence of ovigerous females in the water column during hours of darkness whereas smaller shrimp (predominantly males) persisted in small concentrations in the water column during the morning hours. In the trawl, similarly to BIONESS, the proportion of ovigerous females was significantly higher during bottom trawl tows conducted in hours of darkness (Table 4).

Our results indicate that all sexual groups perform vertical migrations, but with different intensity. At first glance, it may appear paradoxical that the percentage of ovigerous females should increase simultaneously in the BIONESS and in the trawl during the hours of darkness. However, this pattern can be explained by a simultaneous look at the concurrent increase in overall shrimp density in the water column. Since males represent 75% of BIONESS captures, their massive movements off the bottom at night would reduce their abundance on the bottom and result in an increase in the proportion of ovigerous females in the bottom trawl. The simultaneous migration of a comparatively small number of ovigerous females in the water column during the hours of darkness would be sufficient to significantly increase their percentage representation in the BIONESS in comparison with daytime samples (from which they are absent), without major impact on their density on the bottom. This pattern of differential migration is supported by the much lower percentage of ovigerous females captured in the BIONESS (12%) than in the trawl samples (45%).

This interpretation obviously relies on the assumption that the BIONESS and trawl captures accurately reflect the abundance and composition of the shrimp population present in the water column and on the bottom, respectively. The successful capture of some pelagic shrimps in our study suggests that BIONESS catch efficiency was somewhat better than the calculated (negative) value implied. However, absolute shrimp concentrations in the water column could have been extremely high, thus allowing the capture of some shrimp in spite of considerable avoidance. This possibility is strongly supported by comparative results of acoustic echo-integration (Crawford et al. 1992), which further emphasizes the importance of the shrimp pelagic migration. In our study area, shrimp concentrations from BIONESS samples in the 12–70 m stratum above the bottom averaged 23.81 $g \cdot 1000\ m^{-3}$ (5.5 $shrimp \cdot 1000\ m^{-3}$), which is roughly one order of magnitude lower than the average acoustic echo-integration value of 286.11 $g \cdot 1000\ m^{-3}$ (65 $shrimp \cdot 1000\ m^{-3}$) for the same depth interval. In addition, a sharp increase in shrimp concentration occurred in the few metres above the bottom, an area not adequately sampled by the BIONESS. For example, in the depth interval directly above the bottom (0–7 m), average shrimp concentrations for the coffin-shaped area (Fig. 1) derived from trawling and acoustics equalled 1165.68 and 1133.28 $g \cdot 1000\ m^{-3}$ (about 260 $shrimp \cdot 1000\ m^{-3}$), respectively (Parsons et al. 1990). Maximum shrimp concentrations in the same depth interval equalled 5772.19 $g \cdot 1000\ m^{-3}$ (1.3 $shrimp \cdot m^{-3}$) from trawl data and 10511.07 $g \cdot 1000\ m^{-3}$ (2.4 $shrimp \cdot m^{-3}$) from acoustics.

In addition to differences in overall catch efficiency, the use of bottom trawl and BIONESS could also be responsible for the differences in size composition of the catch, since they select in opposite directions: large shrimp could successfully avoid the BIONESS but could be more effectively captured by the large mesh used in the bottom trawl. Our results suggest that small shrimp spent a more important fraction of their time in the water column than large shrimp (Table 3), inducing differences in their vulnerability to each gear type.

In the BIONESS, no differences in individual weight and overall shrimp concentrations were found with depth strata, suggesting that the probability of capturing a shrimp of any sexual group (or of any size) did not vary with depth. This also suggested that the sex and size representation of shrimp captured in the deepest BIONESS net bore more resemblance to other pelagic samples than to those of shrimp captured on the bottom in the trawl sample. This could be due to gear selectivity or to the difference in depth sampled by each gear (trawl: 0–7 m above the bottom; BIONESS net No. 1: 12–37 m above the bottom).

The occurrence of differential migration patterns with shrimp size (sexual groups) was previously inferred from bottom trawl surveys dealing exclusively with the nonmigratory segment of the population. The increased tendency of "smaller" *P. borealis* to migrate from the bottom at night (Barr 1970; Teigsmark 1983) resulted in an overall lower shrimp abundance, a distinct shift in the size distribution towards larger sizes and a higher percentage of ovigerous females on the bottom at night (Fréchette et al. 1984).

Diet and Food Preference

The occurrence of certain prey organisms in shrimp diet appears to depend primarily on their availability, which varies with the diel vertical migrations of shrimp. The relative abundance of each type of planktonic prey in the diet shifts according to local abundance (Fig. 4). Shrimp captured in the plankton had stomachs full of well-preserved planktonic material whereas shrimp captured on the bottom contained small amounts of benthic and digested material. Although planktonic prey were considerably more important than benthic prey, the simultaneous occurrençe of both types in their stomachs indicated that feeding took place in both environments.

The study of stomach contents is made difficult by the typically poor preservation of organisms and their fragmentation in the stomachs. In addition, stomach contents do not accurately represent diet because different food items are not digested at the same rate, and the remains of certain types of organisms are retained and can be identified in the gut far longer than others (Sarda and Valladares 1990). For instance, in this study, soft-bodied animals such as fish, cephalopods, and polychaete species were difficult to identify in the stomachs, although they potentially accounted for a proportion of the amorphous "fleshy material" commonly found in the stomachs. Because of this, chitinous invertebrates and other animals bearing readily recognizable body parts were comparatively overestimated.

The technique of capture is also a source of potential bias in feeding studies. In the case reported here, feeding by shrimp in the BIONESS could be detected in the nets fishing near the bottom, in which shrimp remained for about 20 min by the time the gear surfaced. Feeding in the two bottom nets could have contributed to the sharp difference observed between shrimp captured in the bottom trawl and shrimp sampled a few metres above them in the deepest BIONESS nets. Net feeding also explains the difference of stomach fullness and preservation of the contents between bottom and surface nets. However, even if only surface nets are considered, the stomach contents of pelagic shrimp were always far more abundant and in better condition than those of shrimp sampled on the bottom with the trawl. In addition, evidence of net feeding further supports the extensive use of planktonic prey by *P. montagui*, whenever they have access to this food resource.

In decreasing order of importance, copepods, chaetognaths, and hyperiid amphipods were the most frequent and abundant planktonic prey of shrimps (Table 7). Copepods were abundantly consumed at all depths (Fig. 4) and constituted the staple food of shrimp. It is unlikely that net feeding should have affected the representation of the common prey. Shrimp feeding in the net at the time of capture might have selected specific prey that they could not readily capture under natural conditions, which would increase the frequency of rare prey, resulting in electivity values proportional or superior to the occurrence of the prey in the surrounding zooplankton. The observed preference for certain groups such as pteropods, mysids, cephalopods, and fish reflects the fact that they were the major prey item in a few (<10%) of the stomachs whereas they were rare (or absent) in the corresponding zooplankton sample. Feeding in the net may be at least partially responsible for this apparent preference.

Low electivity (or high preference) values could also be explained by a slow digestion rate of the prey and/or a high mobility of the shrimp, which would allow the prey to remain in the stomach longer than the time necessary for a change in the surrounding zooplankton composition. For instance, cephalopod remains were found in the stomachs of shrimp captured below the depth of occurrence of that prey, indicating that the distribution of shrimp varied more rapidly than the occurrence of digestion and obscuring spatial and temporal variability of feeding preferences. Digestion could be slow in the cold (1.0 to −1.0°C) waters of eastern Hudson Strait. Wienberg (1981) showed that the proportion of identifiable planktonic organisms decreased steadily during the course of the morning whereas diurnal feeding on benthos also took place, resulting in stomachs reaching their maximum fullness in the afternoon. No such periodic changes could be identified from our BIONESS or bottom trawl samples. The occurrence of sand grains in the gut of shrimp captured in the trawl could be accidental, as particles associated with benthic preys, or voluntary, to facilitate digestion and/or egestion, as was previously observed for amphipods (Hargrave 1972; Marchant and Hynes 1981).

Factors Inducing Variability in Vertical Feeding Migrations

The vertical migrations of *P. montagui* coincide with intensive feeding forays in the plankton. Furthermore, the results suggest that the pattern of planktonic incursions varies with shrimp size (sexual groups), small individuals spending more time in the water column than large ones. However, these generalized movements inferred for the population are difficult to interpret in terms of movements by individual shrimp, since the data integrate movements of large groups of individuals (Pearre 1979). More detailed data are required to characterize the ontogenetic changes in migration patterns, which would relate shrimp's food requirements to the extent, duration, and synchrony of planktonic sojourn over the duration of its life cycle.

Previous reports (Apollonio and Dunton 1969; Fréchette and Parsons 1983) suggested reduced vertical migrations of ovigerous females. However, BIONESS captured ovigerous as well as male shrimp up to 200 m above the bottom. The lower proportion (12%) of ovigerous females in the BIONESS than in the trawl (45%) suggests that their occurrence throughout the water column may have been incidental. For example, shrimp could have been entrained passively toward the surface via turbulence, once they reached a critical height above the bottom (benthic boundary layer), thus explaining their irregular distribution in the water column.

A variety of physical factors are likely to exert an influence on pandalid shrimp abundance and vertical migration pattern, potentially explaining the important variability in trawl captures on a local/regional (depth, physiography, and bottom type) and temporal (tidal and residual currents, lunar cycles, and daily and seasonal light cycles) basis. In addition, differences in the amplitude and intensity of vertical migrations of *P. borealis* and *P. montagui* could result from their preference for specific environmental conditions, although both species occur over the same geographical range. For example, *P. montagui* is prevalent in the cold (−1 to 2°C), well-mixed waters of Arctic origin (which become the ''cold intermediate layer'' in the Northwest Atlantic), while *P. borealis* is characteristically found in the deep (150–500 m), warm (2–5°C), stratified layer of Atlantic origin located below the intermediate cold layer. Given the rarity of occurrence of *P. borealis* in waters ≤0°C (Shumway et al. 1985), it is possible that the upper limit of its vertical migration could be determined by the lower edge of the intermediate cold layer.

For pandalid shrimp, the occurrence of important vertical daily migrations results in the unavailability of a variable proportion of the total shrimp biomass to bottom trawls. Furthermore, migrations are carried out with different intensity by the different sexual groups, which rules out the use of the proportion of ovigerous females occurring in bottom trawl samples as a possible standardization method of catch rates over the diel cycle (Anonymous 1978, cited in Parsons and Sandeman 1981). Reliable estimates of the diel fluctuations of pelagic biomass, sexual groups, and size composition are required for effective stock assessment and management of pandalid shrimp species.

The uninterrupted feeding activity by shrimp when they are in the pelagic environment, as well as their use of the most abundant prey, would qualify them as opportunistic feeders, taking advantage of resources as long as they are available. Although this study only documents activity over a 2-wk period, the relative importance of planktonic feeding could also vary seasonally, depending on the zooplankton biomass available for shrimp. It would be of interest to determine if shrimp vertical migrations remain as extensive in the absence of food in the shallow layers. Indirect supporting evidence of a seasonal shift in food sources was reported by Wienberg (1981) and Apollonio and Dunton (1969) for *P. borealis*. Much of the primary productivity that occurs in Arctic waters appears in a short early summer pulse and sinks unutilized by shrimp to the sea floor (Longhurst et al. 1984). Zooplankters relying on this burst of primary production could support shrimp feeding during the summer and fall whereas more seasonally stable benthic resources could sustain shrimp for the rest of the year.

Acknowledgements

The help of Vincent Jarry and Georges Lobb in keeping the BIONESS operational was invaluable. Patrick Veitch, Jack Fife, and John Percy also contributed to the field work. Doug Hope carried out shrimp measurements and Gabriel Lamarche patiently identified shrimp stomach contents. Figures were drafted by Shirley Leach. Yvon Letarte, Guy Préfontaine, and Patrick Veitch helped with data processing and statistical analyses. The authors thank the officers and crew of the fisheries research vessel FRV *Alfred Needler*. The constructive comments of Louise Savard, Dan. M. Carlsson, and Per Kanneworff on an earlier version of the manuscript are acknowledged with thanks.

References

Allen, J. A. 1959. On the biology of *Pandalus borealis* Krøyer, with reference to a population off the Northumberland coast. J. Mar. Biol. Assoc. U.K. 38: 189–220.

1963. Observations on the biology of *Pandalus montagui* [Crustacea: Decapoda]. J. Mar. Biol. Assoc. U.K. 43: 665–682.

Anonymous. 1978. Report on exploratory fishing assessment of pink shrimp fishery potential in northeastern Canadian waters. Prepared for Supply and Services Canada and Fisheries and Environment Canada. MacLaren Marex, Inc. (Available from DFO, Northwest Atlantic Fisheries Center, P.O. Box 5667, St. John's, Nfld. A1C 5X1, Canada)

Apollonio, S., and E. E. Dunton, Jr. 1969. The northern shrimp, *Pandalus borealis*, in the Gulf of Maine. Maine Dep. Sea and Shore Fish. Res. Proj. No. 3-12-R: 82 p.

Barr, L. 1970. Diel vertical migration of *Pandalus borealis* in Kachemak Bay, Alaska. J. Fish. Res. Board Can. 27: 669–676.

Berenboim, B. I. 1981. Feeding of northern shrimp in Barents Sea. Translated from Biol. Morya 5: 28–32.

Canadian Hydrographic Service. 1983. Sailing directions. Labrador and Hudson Bay. 5th ed. DFO, Ottawa, Ont. 450 p.

1988. Tides and current tables. Vol. 4. Arctic and Hudson Bay. DFO, Ottawa, Ont. 450 p.

Carlsson, D. M., Sv. Aa. Horsted, and P. Kanneworff. 1978. Danish trawl surveys on the offshore west Greenland shrimp grounds in 1977 and previous years. ICNAF Sel. Pap. 4: 67–74.

Clutter, R. I., and M. Anraku. 1968. Avoidance of samplers, p. 57–76. *In* D. J. Tranter [ed.] Zooplankton sampling. Monographs on Oceanographic Methodology 2, UNESCO, Paris.

Crawford, R. E., C. Hudon, and D. G. Parsons. 1992. An acoustic study of shrimp (*Pandalus montagui*) distribution near Resolution Island (eastern Hudson Strait). Can. J. Fish. Aquat. Sci. 49. (In press)

Fréchette, J. and D. G. Parsons. 1983. Report of shrimp ageing workshop held at Ste. Foy, Québec, in May and at Dartmouth, Nova Scotia, in November 1981. NAFO. Sci. Counc. Stud. 6: 79–100.

Fréchette, J., S. Pilote, and B. Portelance. 1984. Données sur la distribution verticale de la crevette, *Pandalus borealis*, et ses implications sur les estimations de stocks. Minist. Agric. Pêches Aliment. Dir. Rech. Sci. Tech. Cah. Inf. 107: 48 p.

Hargrave, B. T. 1972. Prediction of egestion by the deposit feeding amphipod *Hyalella azteca*. Oikos 23: 116–124.

Hjort, J., and J. T. Ruud. 1938. Deep sea prawn fisheries and their problems. Hvalradets skrifter 17. Oslo.

Horsted, S.Aa., and E. Smidt. 1956. The deep sea prawn (*Pandalus borealis* Kr.) in Greenland waters. Medd. Komm. Dan. Fisk. Havunders. 1: 1–118.

Hudon, C. 1990. Distribution of shrimp and fish by-catch assemblages in the canadian eastern Arctic in relation to water circulation. Can. J. Fish. Aquat. Sci. 47: 1710–1723.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71.

Longhurst, A., D. Sameoto, and A. Herman. 1984. Vertical distribution of arctic zooplankton in summer: eastern Canadian archipelago. J. Plankton Res. 6: 137–168.

Marchant, R., and H. B. N. Hynes. 1981. Field estimates of feeding rate for *Gammarus pseudolimnaeus* in the Credit River, Ont. Freshwater Biol. 11: 27–36.

Mistakidis, M. N. 1957. The biology of *Pandalus montagui* Leach. Fish. Invest. Ser. II Mar. Fish. G.B. Minist. Agric. Fish. Food 21: 52 p.

Neelakantan, B. 1975. Food and feeding habits of the northern shrimp *Pandalus borealis* from the Oslofjord. Sea Export J. June 1975.

Parsons, D. G., R. Crawford, and C. Hudon. 1990. A hydroacoustical evaluation of the efficacy of bottom trawl surveys for estimating abundance of pandalid shrimp. ICES Shell. Symp. No. 24.

Parsons, D. G., and E. J. Sandeman. 1981. Groundfish survey techniques as applied to abundance surveys for shrimp, p. 124–146. *In* W. G. Doubleday, and D. Rivard [ed.] Bottom trawl surveys. Can. Spec. Publ. Fish. Aquat. Sci. 58: 1–273.

Pearre, S. Jr. 1979. Problems of detection and interpretation of vertical migration. J. Plankton Res. 1: 29–44.

Rasmussen, B. 1953. On the geographic variation in growth and sexual development of the deep sea prawn (*Pandalus borealis* Kr.). Norw. Fish. Mar. Invest. Rep. 57: 1101–1106.

Sameoto, D. D., L. O. Jaroszynski, and W. B. Fraser. 1980. BIONESS, a new design in multiple net zooplankton samplers. Can. J. Fish. Aquat. Sci. 37: 722–724.

Sarda, F., and F. J. Valladares. 1990. Gastric evacuation of different foods by *Nephrops norvegicus* (Crustacea: Decapoda) and estimation of soft tissue ingested, maximum food intake and cannibalism in captivity. Mar. Biol. 104: 25–30.

Shumway, S. E., H. C. Perkins, D. F. Schicks, and A. P. Stickney. 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838. NOAA Tech. Rep. NMSF 30 FAO Fish. Synop. 144: 57 p.

Squires, H. J. 1965. Decapod crustaceans of Newfoundland, Labrador and the Canadian Eastern Arctic. MS Rep. Fish. Res. Board Can. 810: 212 p.

Teigsmark, G. 1983. Population of the deep-sea shrimp (*Pandalus borealis* Krøyer) in the Barents Sea. Fiskeridir. Skr. Ser. Havunders. 17: 377–430.

Wienberg, R. 1981. On the food and feeding habits of *Pandalus borealis* Krøyer 1838. Arch. Fischereiwiss. 31: 123–137.

Removal of Total Phosphorus and Phosphate by Peat Soils of the Florida Everglades

Ronald D. Jones and José A. Amador

Department of Biological Sciences and Drinking Water Research Center, Florida International University, Miami, FL 33199, USA

Jones, R. D., and J. A. Amador. 1992. Removal of total phosphorus and phosphate by peat soils of the Florida Everglades. Can. J. Fish. Aquat. Sci. 49: 577–583.

Traditional estimates of soil and sediment phosphorus retention are based on orthophosphate (PO_4) removal from water by soil or sediment columns under saturated water flow. These techniques may not reflect the P uptake of in situ soils accurately because the PO_4 concentration of through-flowing water is often below detection limits in nonpolluted wetlands during the growing season. We used peat soils from the Florida Everglades in saturated flow and equilibrium sorption experiments to show that the uptake of PO_4 reaches saturation quickly, potentially underestimating soil P binding capacity when compared with total phosphorus (TP) retention. The rate of TP uptake was constant for 2 d, while the rate of PO_4 uptake slowed and followed saturation kinetics. The majority of the TP removed was associated with particles within a 1–20 μm size range. Experiments using both NaCl and nonionic detergent (Triton X-100) as well as batch equilibrium sorption studies indicate that the primary mechanism for TP removal by these soils is not straining. Removal of TP by these soils appears to involve abiotic mechanisms that include both hydrophobic and ionic interactions.

Les estimations classiques de la rétention du phosphore dans le sol et les sédiments sont basées sur l'élimination de l'orthophosphate (PO_4) dissous dans l'eau par des colonnes de sol ou de sédiments dans des conditions d'écoulement saturé. Ces techniques peuvent ne pas représenter précisément le taux de captation du P dans les sols *in situ* étant donné que la teneur en PO_4 de l'eau courante est souvent inférieure aux teneurs qui peuvent être détectées dans les terres humides non polluées au cours de la saison de croissance. Les auteurs ont utilisé de la terre tourbeuse des Everglades de l'État de la Floride lors d'expériences sur l'écoulement à travers un sol saturé et sur la sorption à l'état d'équilibre, expériences visant à prouver que la captation de PO_4 atteint rapidement l'état de saturation. Ainsi, la capacité de liaison du P par le sol peut être sous-estimée lorsqu'elle est comparée à la rétention de phosphore total (PT). Le taux de captation de PT était constant pendant deux jours, tandis que le taux de captation de PO_4 diminuait conformément à la cinétique de saturation. La plus grande partie du PT éliminé était associée à des particules de taille allant de 1 à 20 μm. Les résultats d'expériences réalisées avec du NaCl et du détergent non-ionique (Triton X-100) ainsi que des études par lot de sorption à l'état d'équilibre ont révélé que le filtrage n'est pas le mécanisme primaire d'élimination du PT dans ce type de sol. Elle semble plutôt relever de mécanismes abiotiques comprenant des interactions hydrophobes et ioniques.

Received February 8, 1991
Accepted October 4, 1991
(JA891)

Reçu le 8 février 1991
Accepté le 4 octobre 1991

Phosphorus limits primary production in many freshwater environments (Schindler 1977) and is often considered a pollutant when present in surface water and wetlands at high concentrations (Stumm and Morgan 1981). Phosphorus in freshwater exists in both organic and inorganic forms, which together constitute total phosphorus (TP) (Wetzel 1983). Particulate fractions may be living or nonliving and may be available for plant growth or refractory and unavailable. Organic forms of P exist as cellular components of microorganisms and as particulate organic matter. Inorganic forms of P include phosphatic minerals as well as orthophosphate (PO_4). Free PO_4 comprises only a small fraction of the TP found in unpolluted surface waters during the productive season (Wetzel 1983), yet it is this form that has been used traditionally to assess the P binding capacity of sediment or soil (Syers and Iskandar 1981).

Previous studies of P dynamics in freshwater wetlands have relied on the use of equilibrium isotherms to describe PO_4 retention in soil (Richardson 1985). However, equilibrium studies are often not applicable to field conditions because soils and sediments are nearly always at disequilibrium with respect to ion transformations (Sparks 1989). Furthermore, measuring net changes in concentration provides little information on flux rates of P to and from soil particles. Considering the myriad of potential P forms which may be exchanging with sediment particles, it is misleading to use estimates of P removal by soils using inorganic PO_4 (Richardson 1985).

The Florida Everglades constitute an important, unique ecosystem, not only because of its vastness, but also as a refuge for a number of endangered species (Hendrix and Morehead 1983). Nutrients released into this water by agricultural operations have resulted in increased eutrophication of the Everglades ecosystem (Scheidt 1988). Biological productivity in the Florida Everglades ecosystem has historically been limited by nutrient inputs through rainfall (Scheidt 1988). Phosphorus enrichment of marsh water has resulted in a decrease in the spatial diversity and complexity of the marsh, with native wetland algae and plants being replaced by organisms more tolerant of eutrophic conditions (Scheidt 1988).

In view of the ecological significance of the Everglades and the lack of information on the kinetics of removal of different forms of P by the peat soils of the Everglades, experiments were conducted to see if the apparent kinetics of TP removal from solution under saturated water flow and batch equilibrium conditions differ substantially from those of PO_4.

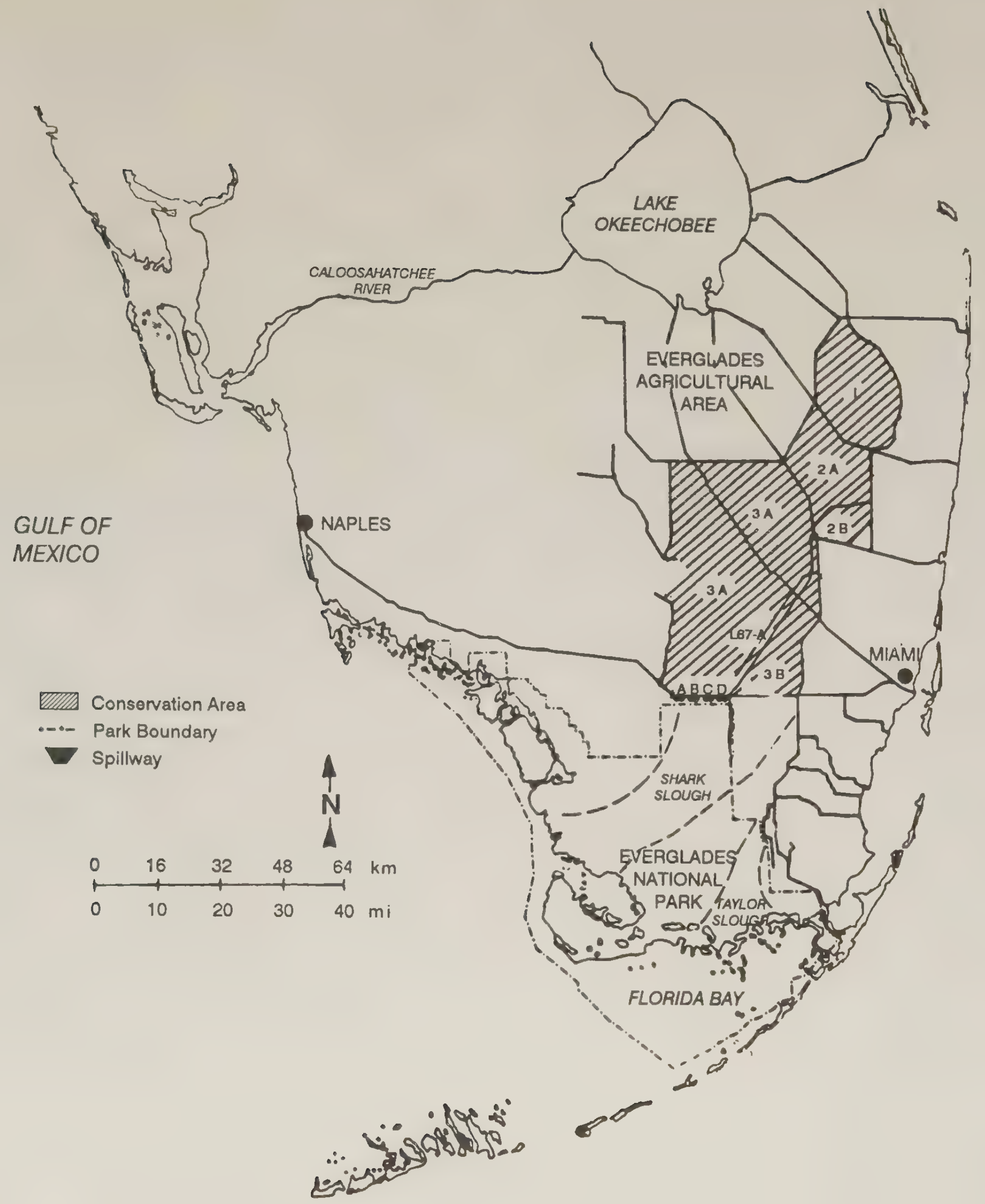

LAKE OKEECHOBEE
CALOOSAHATCHEE RIVER
EVERGLADES AGRICULTURAL AREA
1
2 A
2 B
3 A
3 A
L67-A
3 B
A B C D
GULF OF MEXICO
NAPLES
MIAMI
▨ Conservation Area
•-•- Park Boundary
▼ Spillway
N
0 16 32 48 64 km
0 10 20 30 40 mi
SHARK SLOUGH
EVERGLADES NATIONAL PARK
TAYLOR SLOUGH
FLORIDA BAY

FIG. 1. Map of the Florida Everglades.

Study Area

The Florida Everglades comprise 7500 km^2 of freshwater marshes that have a subtropical climate with alternating wet and dry seasons (Wade et al. 1980) (Fig. 1). The Everglades are subject to sheet flow by flooding waters (Gooselink and Turner 1978), with natural drainage to the south and southwest through broad, shallow sloughs. The Everglades Agricultural Area consists of wetlands drained by four stations that pump water from the agricultural fields into canals that feed southward to the Water Conservation Area (WCA) wetlands. The WCAs (designated 1, 2A, 2B, 3A, and 3B) are shallow-water reservoirs maintained for flood control and water supply. Water from the WCAs is introduced through a series of levees and canals into Everglades National Park, a preserve for wilderness, wildlife habitat, and recreation. The soils in this area are hydric peats formed primarily from the decomposition of sawgrass (*Cladium jamaicense*) and are usually aerobic despite their flooded condition.

Methods and Materials

The following experiments have been repeated on a number of occasions with similar results. Only the experiments conducted on soils collected during early March 1990 will be described in detail here. Experiments were conducted using soil from a pristine area with a 2-km radius within the Shark River Slough (25°35.5′N, 80°43.8′W) not impacted by agricultural runoff. The soil had a pH of 6.6 and contained 88.3% organic matter, 47.4% C, and 3.8% N. Total content of other elements (grams per kilogram of dry soil) were as follows: TP, 0.231; Al, 2.40; Fe, 6.86; Ca, 13.3; and Mg, 0.300 (J. A. Amador et al., unpubl. data).

Marsh water was collected in early March 1990 near a sluice (S-12C) where water enters the Park (Fig. 1). TP was labeled with ^{32}P by adding a trace amount of $^{32}PO_4$ (7.40 MBq, Amersham) to 4 L of unfiltered marsh water containing 1.16 μM TP and a PO_4 concentration of less than 0.02 μM (analytical detection limit). On other occasions at this study site the turnover time for trace levels of PO_4 was calculated to be less than 4 min (R. D. Jones, unpubl. data). The water containing the radiolabeled PO_4 was incubated under cool white fluorescent light for 10 d and filtered through a 20-μm pore-size Nitex screen in order to remove large particles that may introduce a potential error due to straining. Less than 1% of the radioactivity was removed by this step. [^{32}P]PO_4 was used to label TP because it was expected to be equilibrated quickly and evenly by the marsh water microflora and exchangeable P forms. The initial concentration of radiolabeled TP was varied by dilution with buffered salts solution. The buffered salts solution mimicked the pH and concentration of major inorganic ions in the marsh water overlying the soil and contained the following (milligrams per litre): $NaHCO_3$, 23.0; KCl, 0.6; $MgCl_2 \cdot 6H_2O$, 11.0; and $CaCl_2 \cdot 2H_2O$, 46.0. The solution was autoclaved before use and the pH of the solution adjusted to 7.5 with HCl after equilibration with the atmosphere. Measurement of TP concentration and removal rates based on radioactivity and by colorimetric methods described below gave similar results, indicating a constant specific activity value for the major forms of TP.

Apparent kinetics of TP and PO_4 removal by soil were measured under saturated flow conditions (soil saturated at all times) by passing either marsh water containing a known concentration of radiolabeled TP or a buffered salts solution containing a known concentration of $^{32}PO_4$ through a soil column. Soil columns were prepared by placing 2.5 g of wet soil (approximately 0.3 g dry wt) in a 20-mL plastic syringe. A 3-mm-thick polypropylene foam plug was placed at the bottom of the syringe to prevent loss of soil from the column. A second foam plug of the same thickness was placed on top of the column to prevent disturbance of the soil surface. Experiments using foam plugs alone demonstrated that the foam did not remove any TP or PO_4 from solution. The soil column was approximately 1 cm high and had a diameter of 1.8 cm. The soil was washed overnight with buffered salts solution (pH 7.5) containing no P at a flow rate of 30 mL/h in order to equilibrate the pH of the effluent and allow the soil time to settle. Washing the soil in this manner did not remove P from the soil and had no measurable effect on the TP content of the soil. A buffered salts solution (pH 7.5) containing a known concentration of radiolabeled PO_4 or TP was then passed through the column at a rate of 30 mL/h. Tests of the effects of NaCl (50 g/L) and a nonionic detergent, Triton X-100 (10 mL/L), on removal of TP by soil were conducted by washing the soil column with buffered salts solution containing either NaCl or Triton X-100 and then passing buffered salts solution containing radiolabeled TP and either NaCl or Triton X-100. The eluted solution was collected with a fraction collector and individual fractions analyzed for the presence of radiolabeled P.

Unless otherwise noted, P concentration was estimated based on radioactivity measurements. Removal was defined as the difference in ^{32}P activity before and after passage through the soil column, according to the following equation:

$$TP_{removed} = TP_{initial} \times (DPM_{removed}/DPM_{initial}).$$

In contrast with the above experiments where the water or salts solution flowed through the soil, we also conducted batch equilibration experiments where varying amounts of soil and 50 mL of marsh water containing a known concentration of TP were incubated in polyethylene bottles. Bottles were capped and shaken slowly at 25 rpm. Under these conditions the soil formed a thin layer on the bottom of the bottle, with no visible suspension of soil particles. Samples were removed from the overlying water at different times and were analyzed for ^{32}P radioactivity. Phosphate was measured as phosphoantimonyl–molybdenum complex with an absorbance maximum at 880 nm using an RFA-300 Rapid Flow Analyzer (ALPKEM Corp., Clackamas, Oregon, USA). Total P was measured by the method of Solorzano and Sharp (1980). Radioactivity was measured using a liquid scintillation counter (Beckman).

Results

The rate of TP retention by Shark River Slough peat soil under saturated flow conditions was constant for up to 3000 min, i.e. 2 d (Fig. 2). Increasing the concentration of TP to which the soil was exposed from 0.16 to 1.00 μM resulted in an increase in the rate and extent of TP retention by the soil but had no effect on the apparent kinetics, which were linear at all TP concentrations tested ($r^2 = 0.99$). Autoclaving the soil for 1 h increased the rate of retention of 1.0 μM TP but had no effect on the apparent kinetics, which again were linear. In contrast, the rate of removal of 1.0 μM PO_4 by the same soil decreased with time and leveled off after 1500 min (1 d). The extent of removal of 1.0 μM TP by soil was double that of 1.0 μM PO_4 after 1500 min. Release of TP from soils to which TP was previously added occurred at a nearly constant rate approximately 100 times slower than the removal rate.

An experiment was performed to determine the effects of changes in ionic strength and hydrophobicity on removal of TP from marsh water. Addition of NaCl (final concentration 50 g/L) to marsh water containing 0.5 μM radiolabeled TP resulted in a decrease in the rate of TP removal by soil relative to the treatment containing no NaCl, but had no effect on the kinetics of TP removal, which were linear (Fig. 3). The rate and extent of TP removal decreased by 70% in the presence of NaCl. Similarly, the presence of a nonionic detergent, Triton X-100 (final concentration 10 mL/L), had no effects on the kinetics of TP removal, but resulted in an 85% decrease in the rate of TP removal relative to the treatment containing no added detergent (Fig. 3).

Apparent kinetics of TP removal by soil measured in batch equilibrium experiments were unaffected by changes in the ratio of soil to water (range 0.02–0.40; Fig. 4). Changes in the soil to water ratio were achieved by holding constant the volume of water and changing the amount of soil. Removal of TP occurred mostly during the first hour, after which the process continued at a slower, nearly constant rate. No TP removal was observed in treatments containing no soil.

Fractionation of the TP by passage through different pore-size filters (Nuclepore) showed that half of the TP was initially associated with particles of diameter equal to or less than 1 μm before addition to a soil column (Fig. 5). Upon passage of the solution containing TP through a soil column for 56 h, the size distribution of the TP changed dramatically, with 90% of the TP in the eluant associated with particles 1 μm or less in diameter, indicating almost complete removal of particles 5-μm and larger in diameter. Measurements of the particle size distribu-

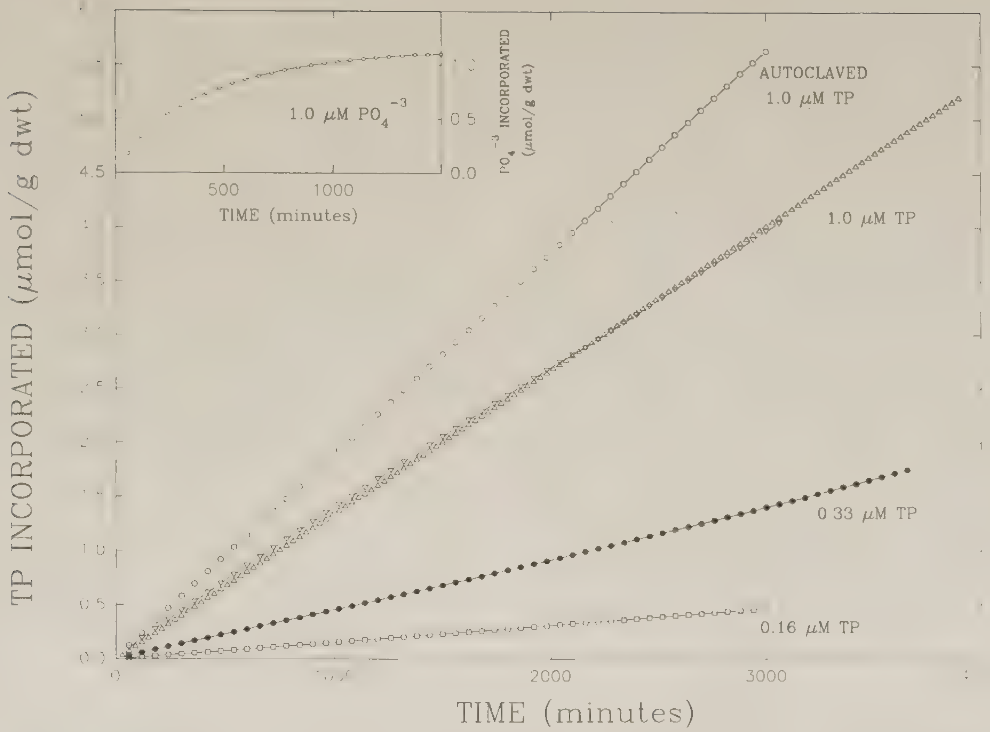


FIG. 2. Apparent kinetics of TP and PO_4 (inset) removal by fresh and autoclaved soil under saturated flow conditions. Inset scale is the same as for the figure. Two replicates are shown for 1.0 µM TP.

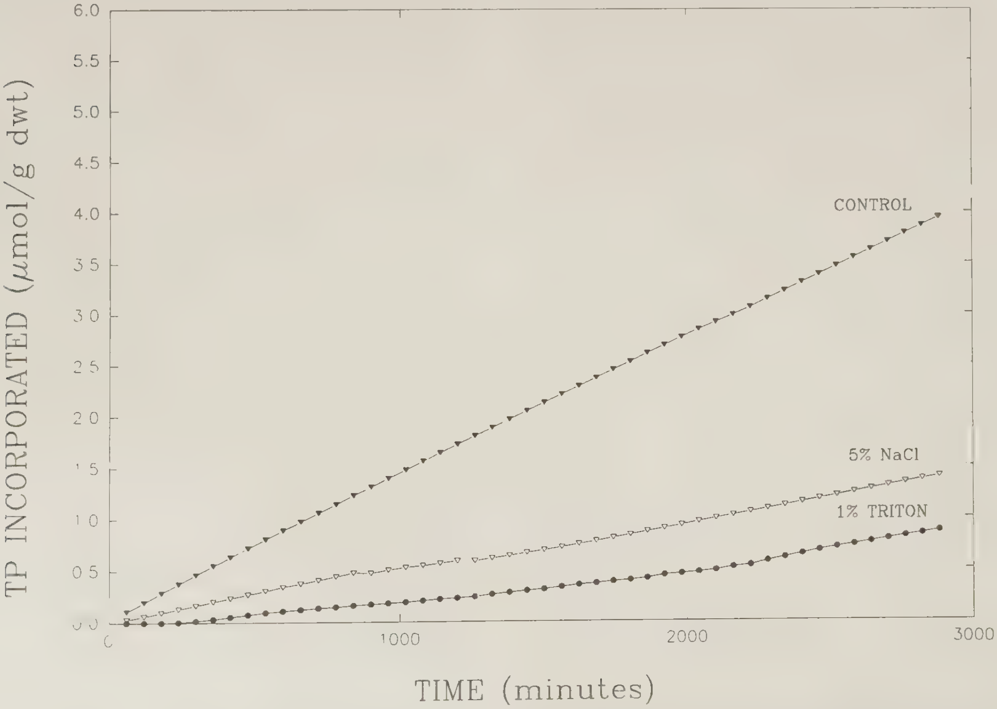


FIG. 3. Effect of addition of NaCl or Triton X-100 on the apparent kinetics of TP removal by soil under saturated flow conditions. Data were normalized to a concentration of 1.0 µM TP for comparison with previous figure.

tion at different times throughout the experiment showed that the resulting size distribution pattern was the same regardless of elution time. Only particles with a diameter of 5 µm or less were eluted by washing the column with buffered salts solution. Particle size distribution of TP in the supernatant solution from batch equilibrium experiments exhibited a pattern similar to that observed in the eluant from soil column experiments, that is, particles with a diameter of less than 1 µm were removed to a lesser extent by the soil whereas particles with a diameter greater than 5 µm were removed to the greatest extent. The total amount of TP removed by the soil in column and batch experiments was nearly the same in both cases (inset, Fig. 5).

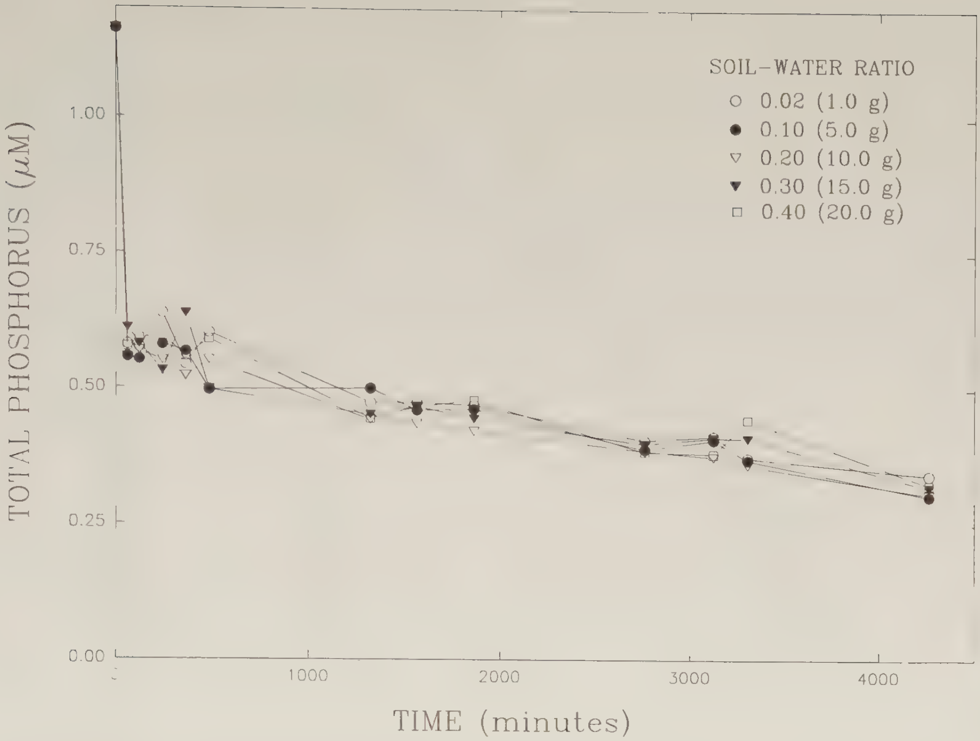


FIG. 4. Removal of TP from solution by soil at different soil to water ratios in batch equilibrium experiments. Initial P concentration was 1.16 μM for all treatments.

A mass balance on P associated with different particle size classes before and after soil column and batch equilibrium experiments was performed (Table 1). These results show that similar amounts of P were removed under both experimental conditions for particles sizes including <0.2, 1–5, and 12–20 μm. The amount of P removed in the 0.2–1 μm diameter range was more than 10 times greater in the batch than in the column experiment whereas a lower extent of P removal was observed for particles in the 5–12 μm diameter range under batch equilibrium conditions relative to the column experiment.

Discussion

Kinetics of PO_4 removal by soil are often described as having a fast initial phase followed by a slower second phase (Enfield and Ellis 1983). Our results indicate that removal of TP from soil is described by simpler kinetics, apparently involving a process or processes whose rate is constant with time for almost 3 d. The mechanisms involved in TP removal by these soils are of obvious interest. The absence of saturation of the soils within the time and TP concentrations tested in both saturated flow and batch equilibrium experiments suggests that abiotic processes are involved in TP removal. While saturation is certainly a possibility at extended elution times even for abiotic processes, saturation was not observed within the time frame studied. The absence of an effect of autoclaving the soil on kinetics of TP removal further supports this point.

The preferential removal of TP particles with a diameter greater than 1 μm observed in saturated flow experiments could be construed as evidence for a removal mechanism involving physical straining of the larger particles. However, a similar preferential enrichment of such particles was observed in batch equilibrium experiments. The small differences observed in extent of TP removal between saturated flow and batch equilibrium conditions, particularly in the 1–5 μm diameter range, may be ascribed to resuspension under batch equilibrium conditions. In order for straining to occur, particles must be forced unidirectionally against a retaining porous matrix. This is clearly not possible under batch equilibrium conditions. Furthermore, if a straining process were primarily responsible for TP removal, prolonged passage of the solution containing TP should result in breakthrough of TP particles. This was not observed in our experiments. Our results indicate that, while straining may be involved to some extent, other mechanisms are likely to be responsible for the majority of TP removal by these soils.

Because of their size, microorganisms are likely to form a large portion of the TP particles removed by the soil. Thus, the mechanisms controlling attachment and detachment of microorganisms to and from soil may control TP removal by soil. Cell size may be involved presumably because large bacteria are less likely to pass through soil pores than are small bacteria. However, studies by Gannon et al. (1991) showed that factors other than cell size control movement of bacteria through soils. The decrease in TP removal by soil resulting from addition of NaCl and detergent indicates that both hydrophobic and ionic interactions may be involved in TP removal. Hydrophobic interactions may be particularly important in the removal of larger particles, which tend to have a higher degree of hydrophobicity than smaller particles, for which ionic interactions may be more important. Microbial attachment and sorption of large organic molecules and particles to soil surfaces is often dominated by these two types of interactions (Marshall 1976). A removal mechanism involving such interactions is consistent with the absence of saturation observed in our experiments. Furthermore, the greater extent of removal of particles in the bacteria size range (0.2–1 μm in diameter) under batch equilibrium conditions relative to saturated flow conditions supports

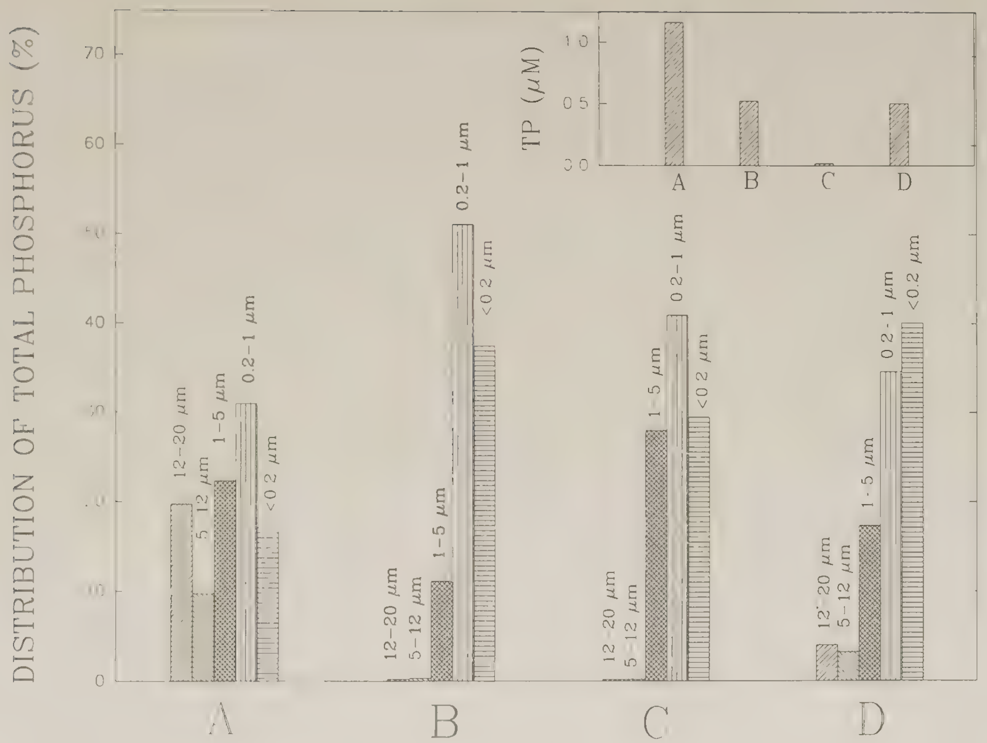


FIG. 5. Effect of removal of TP by a soil column and by equilibration with soil in batch experiments on particle size distribution of TP. Inset shows the concentration of TP in water for the different samples. (A) Initial particle size distribution of TP in marsh water; (B) distribution of eluted TP in water after passage through a soil column; (C) distribution of TP in eluant resulting from washing of the soil column; (D) distribution of TP in supernatant water after equilibration with soil in batch equilibrium experiments.

TABLE 1. Mass balance on P associated with different particle size classes of radiolabeled TP before and after saturated flow and batch equilibrium sorption experiments.

	P (μM) in size class:					
Treatment	<0.2 μm	0.2–1 μm	1–5 μm	5–12 μm	12–20 μm	Total
Saturated flow						
Initial	0.28	0.28	0.35	0.05	0.20	1.16
Final[a]	0.19	0.26	0.06	0	0	0.52
Amount removed	0.09	0.01	0.29	0.05	0.20	0.64
% removed	32.1	3.6	82.8	99.7	99.9	55.2
Batch equilibrium[b]						
Initial	0.28	0.28	0.35	0.05	0.02	1.16
Final[c]	0.20	0.17	0.09	0.20	0.02	0.50
Amount removed	0.08	0.11	0.26	0.03	0.18	0.66
% removed	28.6	39.3	74.3	68.0	90.0	56.9

[a] After 48h.
[b] Experiment was conducted using 5 g of soil in 50 mL of water.
[b] After 56 h.

the argument for mechanisms requiring longer contact times, such as hydrophobic and ionic interactions, being responsible for the removal of these particles from solution. In the absence of evidence suggesting expenditure of metabolic energy by the microorganisms in attachment to soil particles, the process involved in removal must be termed abiotic, as is the removal of organic and inorganic particles from solution by physicochemical processes.

Our data on kinetics of TP removal are likely to describe P dynamics in Everglades soils more adequately than data from sorption isotherms using only PO_4. This is particularly relevant, since the bulk density of these flooded soils is generally less than 0.3 g/cm^3 and much of the surface water is in direct contact with this highly porous matrix. Furthermore, much of the water in this system flows vertically as well as horizontally through these soils. Differences in the apparent kinetics and mechanisms of TP and PO_4 removal have potential ecological and environmental consequences. For example, studies of the kinetics and mechanisms of PO_4 removal by wetland soils cannot be assumed to represent those for other forms of P. Furthermore, measurements of PO_4 removal by soil are likely to underestimate the rate and extent to which P retention occurs. This can have serious effects on oligotrophic wetlands such as the Florida Everglades.

Acknowledgments

This work was supported by the National Park Service, United States Department of the Interior, South Florida Research Center, Everglades National Park, under CA-5280-8-8007. We thank Dr. David Lean for fruitful discussions and suggestions and the three anonymous reviewers for their constructive criticisms.

References

ENFIELD, C. G., AND R. ELLIS. 1983. The movement of phosphorus in soil, p. 93–107. *In* D. W. Nelson [ed.] Chemical mobility and reactivity in soil systems. SSSA Spec. Publ. 11, ASA & SSSA, Madison, WI.

GANNON, J. T., V. B. MANILAL, AND M. ALEXANDER. 1991. Relationship between cell surface properties and transport of bacteria through soil. Appl. Environ. Microbiol. 57: 190–193.

GOOSELINK, J. G., AND R. E. TURNER. 1978. The role of hydrology in freshwater wetland ecosystems, p. 63–78. *In* R. E. Good, D. F. Wigham, and R. L. Simpson [ed.] Freshwater wetlands: ecological processes and management potential. Academic Press, Inc., New York, NY.

HENDRIX, G., AND J. MOREHEAD. 1983. Everglades National Park — an imperiled wetland. Ambio 12: 153–157.

MARSHALL, K. C. 1976. Interfaces in microbial ecology. Harvard University Press, Cambridge, MA. 152 p.

RICHARDSON, C. J. 1985. Mechanisms controlling phosphorus retention capacity in freshwater wetlands. Science (Wash., DC) 228: 1424–1427.

SCHEIDT, D. J. 1988. Nutrient enrichment in the Everglades. Natl. Wetlands Newsl. (May–June): 5–7.

SCHINDLER, D. W. 1977. The evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

SOLORZANO, L., AND J. H. SHARP. 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. Limnol. Oceanogr. 25: 754–758.

SPARKS, D. L. 1989. Kinetics of soil chemical processes. Academic Press, Inc., New York, NY. 210 p.

STUMM, W., AND J. J. MORGAN. 1981. Aquatic chemistry. 2nd ed. John Wiley & Sons, Inc., New York, NY. 780 p.

SYERS, J. K., AND I. K. ISKANDAR. 1981. Soil-phosphorus chemistry, p. 571–599. *In* I. K. Iskandar [ed.] Modelling wastewater renovation. John Wiley & Sons, Inc., New York, NY.

WADE, D., J. EWEL, AND R. HOFSTETTER. 1980. Fire in south Florida ecosystems. USDA Forest Service, Ashville, NC. 125 p.

WETZEL, R. G. 1983. Limnology. 2nd ed. W. B. Saunders Co., Philadelphia, PA. 767 p.

Effects of Multiple Fires on Nutrient Yields from Streams Draining Boreal Forest and Fen Watersheds: Nitrogen and Phosphorus

S. E. Bayley,[1] D. W. Schindler,[2] K. G. Beaty, B. R. Parker,[2] and M. P. Stainton

Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, Man. R3T 2N6, Canada

Bayley, S. E., D. W. Schindler, K. G. Beaty, B. R. Parker, and M. P. Stainton. 1992. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus. Can. J. Fish. Aquat. Sci. 49: 584–596.

Wildfire in the boreal forests at the Experimental Lakes Area in Ontario caused significant losses of nitrogen and phosphorus in streams. Both watershed type and fire intensity appear to determine the extent of losses. The Northeast wetland basin lost more N and P, especially TDN, TDP, TN, and TP, than did terrestrial basins, although nitrate losses were higher from terrestrial basins. Losses of nutrients after the second fire generally were not as high as after the first fire. In the East basin, which burned twice with a high fire intensity, stream concentrations of NO_3^-, TDN, and TN were elevated for 6 yr between the fires and remained elevated for 9 yr after the second fire. In contrast, the Northwest basin burned with a lower intensity and had no significant increase in annual concentrations of P or most forms of N in the first 3 yr after the fire; only NO_3^- concentrations increased during this period. Despite the increases in export after wildfire, net retention of TN and TP over the 18-yr period was high. In the Northeast, East, and Northwest basins, retention of TN averaged 77, 80, and 87% compared with TP retention of 51, 67, and 84%.

Des feux échappés dans les forêts boréales de la zone des lacs expérimentaux de l'Ontario ont entraîné des pertes importantes d'azote et de phosphore dans les cours d'eau. Le type de bassin versant et l'intensité du feu semblent tous deux déterminer l'ampleur des pertes. Le bassin nord-est des terres humides a perdu une plus grande quantité de N et de P, surtout du NDT, du PDT, du NT et du PT, que les bassins terrestres, quoique les pertes de nitrate étaient plus importantes dans les bassins terrestres. Les pertes de bioéléments après le deuxième feu étaient en général moins élevées qu'après le premier feu. Dans le bassin est, qui a été deux fois l'objet d'un feu de forte intensité, les concentrations de NO_3^-, de NDT et de NT ont été élevées pendant les 6 ans séparant les feux, et le sont demeurées pendant 9 ans après le deuxième feu. Par contre, le bassin nord-ouest a été l'objet d'un feu de moindre intensité et n'a pas montré d'augmentation marquée des concentrations annuelles de P ou de la plupart des formes de N au cours des trois années après le feu; seules les concentrations de NO_3^- ont augmenté pendant cette période. Malgré l'augmentation des teneurs en bioéléments exportés après les feux échappés, la rétention nette de NT et de PT pendant ces 18 ans a été élevée. Dans les bassins nord-est, est et nord-ouest, la rétention de NT a atteint en moyenne 77, 80 et 87 %, respectivement, pour une rétention de PT de 51, 67 et 84 %.

Received January 29, 1991
Accepted October 10, 1991
(JA880)

Reçu le 29 janvier 1991
Accepté le 10 octobre 1991

Fire is an important pertubation in terrestrial ecosystems in the boreal forest. Natural wildfires commonly occur at a frequency of one to several times per century in the southern boreal forest (Heinselman 1973; Swain 1973; Clark 1990). In addition, prescribed burning following clearcutting is used extensively in forest management. In the southeast United States, prescribed fires did not cause an increase in chemical concentrations in downstream waters (Richter and Ralston 1982). However, most studies of the effect of fire on the chemistry of surface soil report increased concentrations of NH_4^+, P, K^+, Na^+, and Mg^{2+} for several months after a fire (DeByle and Packer 1972; McColl and Grigal 1975, 1977; Smith and James 1978). There are few studies documenting the effect of wildfire in boreal forests on stream chemistry (Wright 1976; Schindler et al. 1980). A few studies of wildfire in temperate and mountain ecosystems have shown increased concentrations of various ions in streams (Brown et al. 1973; Wright 1976; Tiedemann et al. 1978). Most of the published studies on fire emphasize effects on hydrologic budgets and sedimentation (Tiedemann et al. 1978, 1979; Riekerk 1983; Megahan 1983). Studies of the effects of wildfire on nutrient budgets which include pre- and postburn data for the same watershed are rare (Schindler et al. 1980) and none reports data for more than 3 yr after a fire. Nutrient budgets have been constructed for a variety of forest management strategies (Likens et al. 1970; Johnson and Swank 1973).

The purpose of this paper is to describe nitrogen (N) and phosphorus (P) budgets in three small boreal watersheds before and after forest fires. We will describe long-term effects of a 1974 fire in the boreal watersheds (first described by Schindler et al. 1980) and will describe the effects of a 1980 fire in the same basins. In addition, we compare 9 yr of prefire data on one stream with 9 yr of postfire data on the same stream. We will also describe the effects of these fires on the chemical budget of the adjacent oligotrophic lake. Our objectives are to compare the retention and loss of N and P in the two terrestrial and one wetland watersheds. We compare the effects of fire on these watersheds with other published fire studies and with forest management techniques such as clearcutting and herbicide application (Likens et al. 1970; Johnson and Swank 1973; Aubertin and Patric 1974; Bormann et al. 1974; Feller and Kimmins 1984; Swank 1987).

---

[1] Present address: Department of Botany, University of Alberta, Edmonton, Alta. T6G 2E9, Canada.

[2] Present address: Department of Zoology, University of Alberta, Edmonton, Alta. T6G 2E9, Canada.

Materials and Methods

The Study Watersheds

The study area is in the Experimental Lakes Area (ELA) of northwestern Ontario (lat. 49°40′N, long. 93°44′W). The watershed of Rawson Lake (Lake 239) is composed of three distinct stream drainages (referred to here as subbasins), plus an area which drains directly to the lake (Fig. 1). All three subbasins are underlain primarily by pink granodiorite composed of 40% quartz, 40% plagiocase, and 10% K-feldspar, with traces of ilmenite, muscovite, and kaolinite (Brunskill and Schindler 1971). Lower lying areas and valley bottoms are typically occupied by orthic brunisols, underlain by sand and boulder till which are from a few centimetres to a few metres in thickness.

The Northwest (NW) subbasin (56.4 ha) drains directly to a 120-m stream segment, through a 2-ha wetland, and enters the lake over a V-notch weir. The East (E) subbasin (170.3 ha) is larger than the NW subbasin and more complex, with a much longer (1100 m) stream segment. While there is a small boggy area high in the watershed, 80% of the surface is upland. The Northeast (NE) subbasin (12.43 ha) contains an acid bog (pH 3.9–4.5), which occupies 30% of the basin, into which all upland areas drain. The bog outflow collects in a short stream channel monitored by a weir and then disperses over surface rocks into the lake.

The Fires

The 1973 Windstorm and 1974 fire

On July 7, 1973, a powerful windstorm accompanied by a severe thunderstorm struck the experimental watersheds. Estimated blowdown was less than 20% in the NW subbasin but 50–100% in the other two subbasins. Blowdown was most severe on the hilltops. Trees in the bog areas in the NE subbasin were relatively untouched.

On June 26, 1974, an extremely hot forest fire burned both the NE and E subbasins. The flame-front intensity was 13 000 $kw \cdot m^{-1}$ (Schindler et al. 1980). Virtually all vegetation less than 2.5 cm in diameter was consumed, and organic matter in surface soils was mineralized to a depth of several centimetres. In the NE subbasin, the southern end (35%) of the bog burned as well as upland areas. The NW subbasin was not touched by the fire.

The 1980 fire

On June 20, 1980, a second forest fire occurred in the Lake 239 (L239) basin. Set by a lightning strike to the SW of the L239 watershed, the fire swept up both sides of the lake. On the east side of the lake, in the E subbasin, much of the timber killed in the 1974 fire had fallen, lying criss-crossed in a layer up to a metre deep, with a new, thick cover of *Populus tremuloides* Michx., *Pinus banksiana* Lamb., and herbaceous vegetation reaching up to 2 m in height. This provided fuel for a very hot, fast-moving fire in the E subbasin, which consumed almost all of the vegetation, leaving bare bedrock with isolated pockets of thin overburden. Almost all organic matter in the soils was also combusted.

Approximately 50% of the upland portion of the NE subbasin burned in the 1980 fire, but the wetland and some adjacent upland did not burn.

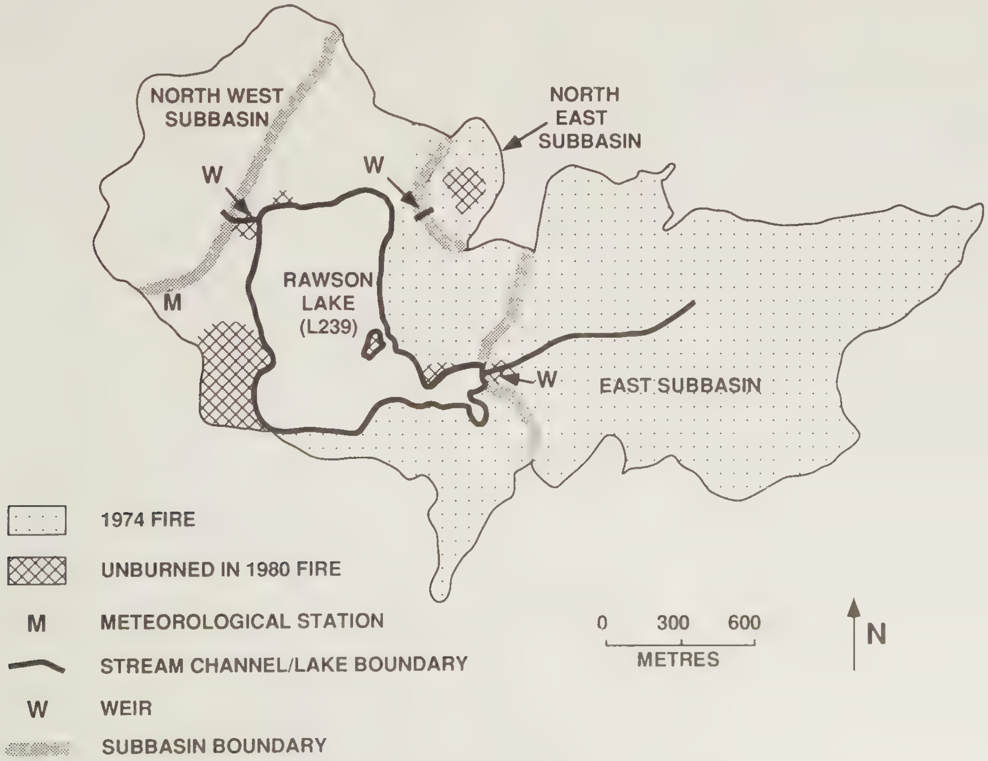


FIG. 1. The L239 watershed at ELA showing the NW, NE, and E subbasins. Grey areas burned in 1974. All of the L239 watershed burned in 1980 except for the hatched areas.

The NW subbasin was burned in the evening and overnight on June 21. Winds were low and humidity was high. As a result, vegetation was killed, but little was consumed. Needles and leaves were left intact on trees and many shrubs. Figure 1 shows the extent of both the 1974 and 1980 fires. For a year after the 1980 fire, black clouds of charcoal and dust reduced visibility in the area on windy days.

Vegetation before and after the Fires

Before the fires, hilltops and steep slopes were thinly forested, while less steeply sloping areas were thickly forested and covered with moss and lichens to a depth of a few centimetres. Before the fires, all upland areas were vegetated by a mature virgin community of jackpine (*Pinus banksiana*) and black spruce (*Picea mariana* (Mill.) BSP), with paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides*) also abundant. Red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and white spruce (*Picea glauca* (Moech) Voss) were also present in small numbers.

After the first fire in the E and NE subbasins, all areas revegetated rapidly. Small jackpine, black spruce, poplar, birch, balsam poplar (*Populus balsamifera* L.), and pin cherry (*Prunus pensylvanica* L.) were present. Dense herbaceous and shrub vegetation was dominated by fireweed (*Epilobium angustifolium* L.), black bindweed (*Polygonum convolvulus* L.), blueberry (*Vaccinium* spp.), and raspberry (*Rubus strigosus* (Michx.)). Within 3 yr after the fire, jackpine stands were so dense as to be almost impenetrable, except in high, rocky areas of the E subbasin where cones were totally combusted. Revegetation of the NW subbasin after the 1980 fire (the only fire in that subbasin) was also rapid.

After the second fire, revegetation in the E subbasin was very slow. Some ridgetop areas had almost no plant cover (<1 plant in 100 m^2) 2 yr later. Lower-lying areas were sparsely covered with jackpine, trembling aspen, pin cherry, saskatoon (*Amelanchier alnifolia* Nutt.), and balsam poplar. Herbaceous and shrub cover, of the above-mentioned species, was also very sparse.

While upland areas of the NE subbasin were very similar to those of the E subbasin after the second fire, the vegetation in the boggy areas of the NE subbasin was little affected by the fire and was (and still is) dominated by black spruce and *Sphagnum* species, chiefly *Sphagnum fuscum* (Schimp.) Klinggr., *S. angustifolium* (Russ.) C. Jens., and *S. magellanicum* Brid. Some trees in the bog were killed, and surface *Sphagnum* was scorched in places. Except for black spruce trees, recovery was rapid in the bog, and Vitt and Bayley (1984) detected no difference in understory vegetation in the burned and unburned portions of the bog. After the 1974 fire, jackpine invaded the southerly (downstream) end of the bog, while the upper end still has an open stand of black spruce.

Data Collection and Analyses

Hydrologic and chemical budgets

Water flows in the NW and E subbasins were measured continuously with weirs and stage recorders during the ice-free season. The NW subbasin weir was installed in 1970. The E subbasin weir was installed in mid-June 1971. The NE subbasin was measured intermittently from 1971 to 1973; in 1974, a continuous recorder was installed. Regressions of E or NE flow versus NW flow were used to estimate daily flow from E and NE weirs during periods of missing record. Winter discharge of water was rare in all three subbasins and measured manually when necessary. A year-round weir at the outlet of L239 and a level recorder on the lake provided a check on hydrological measurements. All precipitation and stream discharge data are presented based on a water year (November 1 through October 31).

Water samples for chemical analyses were collected weekly during the ice-free season (May–October) at the weir in each subbasin. Samples also were taken occasionally in early spring, fall, and winter. During spring melt, there was an intensive sampling effort (see later). Chemical methods are reported in Schindler et al. (1976, 1980) and Stainton et al. (1977).

The chemical budgets for the subbasins were calculated by estimating the daily chemical concentration (based on linear interpolations between weekly chemical measurements) and multiplying these by daily water flows. Mean annual concentrations are volume-weighted concentrations for each year calculated from the total export divided by the total water flow. Monthly concentrations and annual exports of mass are similarily calculated. The budget data (1970–76) presented in Schindler et al. (1980) have been recalculated and include better estimates of spring melt and October and November hydrology.

Weekly water sampling may lead to poor representation of stormflow chemistry relative to base flow conditions and thus give only poor estimates of annual mass transport. This probably has not produced a significant bias in the annual subbasin budgets at ELA for the following reasons: (1) while the rising limb of the storm hydrographs generally had increased concentrations of NO_3^-, total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), suspended nitrogen (Susp N), and suspended phosphorus (Susp P), the peak flow and falling limb had lower concentrations than the base flow and the volume-integrated concentrations were usually only slightly higher than base flow conditions and (2) there was no statistically significant relationship between flow and concentration in the NW subbasin (unburned period 1971–79, $n = 288–330$) for the following parameters: NO_3^- ($r^2 = 0.0006$), NH_4^+ ($r^2 = 0.0000$), TDN ($r^2 = 0.0005$), and TDP ($r^2 = 0.0019$). Susp P concentrations significantly correlated with flow at a low level ($r^2 = 0.027$) in the NW subbasin during the prefire years and therefore the failure to measure flows following some storms could result in a slight underestimation of annual export of Susp P. Flows and concentrations during many of the large storms were actually measured, so it is the small to medium-sized summer and fall storms that could cause an underestimation, but this is unlikely to be serious because the relationship between flow and concentration for summer and fall was poor (Susp P had $r^2 = 0.054$ and $n = 231$). Bias in mass export generally did not occur during the high flows in spring melt since these were measured. According to Johnson (1979), acceptable estimates of annual mass flux can be obtained from samples collected weekly provided all flow stages are represented.

Statistical approach and analysis

To perform statistical analyses of subbasin exports and streamwater concentrations before and after fires, masses exported and streamwater concentrations were calculated on the basis of the fire (and windstorm) events. The events occurred on July 7, 1973 (windstorm), June 26, 1974 (first fire), and June 20, 1980 (second fire). The following time periods for the NE and E subbasins were used in Tables 1–5. Prefire period:

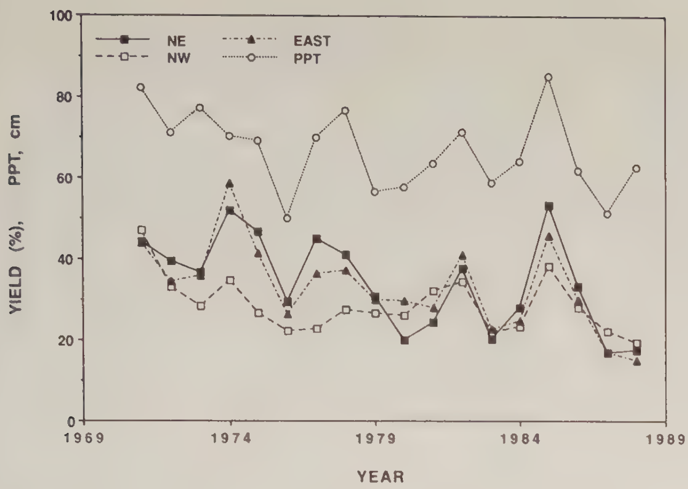


FIG. 2. Annual yield from the three ELA streams and annual precipitation from 1971 to 1989.

June 1971 to July 6, 1973; windstorm period: July 7, 1973 to June 25, 1974; postfire period 1a: June 26, 1974 to June 25, 1977; postfire period 1b: June 26, 1977 to June 19, 1980; postfire period 2a: June 20, 1980 to June 19, 1983; postfire period 2b: June 20, 1983 to June 19, 1986; postfire period 2c: June 20, 1986 to June 20, 1989.

In the NW subbasin, the prefire period was 9 yr (June 1971 to June 19, 1980) and the 9 yr of the postfire period then follow as described for periods 2a, 2b, and 2c above.

To determine statistically the effect of fires on chemical exports and streamwater concentrations, a Student *t*-test was used to test the null hypothesis that the mean of the exports (for streamwater concentrations) for the postfire periods was the same as that prior to the fire. If the test statistic was significant at $\alpha = 0.05$, then the postfire period was considered significantly different from the prefire mean.

Statistical analysis of the impact of fire on the seasonal concentrations of nutrients was similarly performed. Monthly concentrations and standard errors were calculated for all prefire years and compared with the mean monthly concentrations and standard errors in the 3 yr after fire. For the NW subbasin, the postfire period was June 24, 1980 to October 26, 1983. Prefire years are calculated from data from 1971 through June 19, 1980. For the E and NE subbasins, the period of June 17, 1974, to November 30, 1977, was considered to be ''postfire.'' Any recovery during this period was ignored. Likewise, effects of the 1973 windstorm are ignored and because of this, interpretations of seasonal fire effect are conservative.

To present the effect of fires visually (in Fig. 2–4), volume-weighted mean annual concentrations were calculated starting in late June to avoid bias due to the late June fires.

Results

Changes in Basin Exports after Fire

Water yields

Annual precipitation varied almost twofold, from 854 mm in 1985 to 500 mm in 1976 (Fig. 2). The high interannual variability in rainfall made interpretation of the effects of fires on water yield difficult because the basins were responding to a variety of changes in vegetation and soil moisture, temperature, evapotranspiration, and wind velocity. In particular, below-average annual precipitation from 1979 to 1988 (except 1982 and 1985) followed the fire years and confounded simple interpretations (Fig. 2). In addition, the windstorm in 1973 caused increased yield of water (Schindler et al. 1980).

However, the effect of the 1974 fire and the 1973 windstorm can be seen by comparing the increased yield from the wind-damaged and burned NE and E subbasins with the lower yield in the same years from the unburned and slightly wind-damaged NW subbasin (Table 1). The yield remained higher in the NE and E subbasins compared with the unburned NW subbasin for 5 yr after the fire (individual years not shown).

By 1979, annual water yields in the NE and E subbasins were close to that from the unburned NW basin (individual years not shown). After the 1980 fire in which the NW subbasin burned as well, yields increased in the NW and E subbasins (Table 1). The water yield from the E basin after the second fire was lower than the yield after the first fire.

The water yield from the wetland basin after the 1980 fire (1980–83) was less than the yield after the 1974 fire (1974–77) for two possible reasons: the precipitation in 1978–83 was lower than in the early 1970's creating a greater storage deficit in the past, and the wind speed was higher causing higher evapotranspiration.

Changes in Chemical Exports after Fire

In the NW subbasin, annual export of NO_3^- was low and variable until the 1980 fire. In 1981, 1 yr after the fire, exports

TABLE 1. Precipitation, discharge, and yield (discharge/precipitation) on an annual basis in three ELA watersheds during the periods before and after fires (data in mm of water). The symbol † denotes significantly ($p > 0.95$) higher and ◇ denotes significantly lower than the prefire period (June 1971 to June 1973) in the NE and E subbasins. Double underline denotes when the first fire occurred.

Period	No. of years	Annual precipitation	Annual discharge			Annual yield		
			NW[a]	E	NE	NW[a]	E	NE
Prefire	2	743.1	266.9	267.4	286.4	0.359	0.360	0.385
Windstorm	1	849.4	325.9	436.8	393.1	0.384	0.514	0.463
Postfire 1a	3	630.5◇	151.5	238.7	281.2	0.239	0.373†	0.445
Postfire 1b	3	614.2	156.9	213.8	219.5	0.243	0.335◇	0.336
Postfire 2a	3	668.6◇	221.1	228.5	187.7◇	0.328	0.338◇	0.274
Postfire 2b	3	675.9	213.3	257.5	282.3	0.307	0.369	0.402
Postfire 2c	3	615.8◇	147.3◇	117.9◇	133.7◇	0.229◇	0.185◇	0.208

[a] In the NW watershed, fire did not occur until period 2a and the statistical comparisons are based on a prefire period of 1971–80.

TABLE 2. Input, export, and retention of N in the three ELA watersheds before and after fire (data in kg·ha^{-1}·yr^{-1}). %*R* = % retention. The symbol † denotes data significantly higher ($p > 0.95$) and ◇ denotes data significantly lower than the prefire period (June 1971 to June 1973) in the NE and E subbasins. Double underline denotes when the first fire occurred.

Period	No. of years	Input	NW[a] Export	NW[a] Retention	NW[a] %*R*	E Export	E Retention	E %*R*	NE Export	NE Retention	NE %*R*
					NO_3^-						
Prefire	2	4.22	0.035	4.185	99	0.061	4.159	99	0.017	4.203	99
Windstorm	1	1.71	0.049	1.661	97	0.175	1.535	90	0.034	1.676	98
Postfire 1a	3	1.72◇	0.051	1.669	97	0.420†	1.300	76	0.041†	1.679	98
Postfire 1b	3	1.62◇	0.026	1.594	98	0.110†	1.510	93	0.006◇	1.614	99
Postfire 2a	3	2.03◇	0.292†	2.000	99	0.187†	1.843	91	0.023†	2.000	99
Postfire 2b	3	2.94◇	0.059	2.881	98	0.142†	2.798	95	0.019	2.921	99
Postfire 2c	3	2.51◇	0.102†	2.408	96	0.109†	2.401	96	0.021	2.489	99
					NH_4^+						
Prefire	2	3.38	0.036	3.340	99	0.043	3.337	99	0.052	3.328	98
Windstorm	1	1.77	0.051	1.719	97	0.099	1.671	94	0.106	1.664	94
Postfire 1a	3	1.73◇	0.028	1.702	98	0.089†	1.641	95	0.114†	1.616	93
Postfire 1b	3	1.57◇	0.030	1.540	98	0.049	1.521	97	0.048	1.522	97
Postfire 2a	3	2.25◇	0.051	2.199	98	0.055†	2.195	98	0.047	2.203	98
Postfire 2b	3	2.61◇	0.070	2.540	97	0.114†	2.496	96	0.111†	2.499	96
Postfire 2c	3	2.34◇	0.046	2.294	98	0.048	2.292	98	0.038	2.302	98
					TN						
Prefire	2	10.18	0.820	9.360	92	1.029	9.151	90	1.185	8.995	88
Windstorm	1	5.53	1.060	4.470	80	1.797	3.733	68	1.993	3.537	64
Postfire 1a	3	5.94◇	0.709	5.230	88	1.824†	4.116	69	2.051†	3.889	65
Postfire 1b	3	5.13◇	0.713	4.417	86	1.193	3.937	76	1.372	3.758	73
Postfire 2a	3	7.44◇	1.141†	6.269	84	1.389†	6.051	81	1.381	6.059	81
Postfire 2b	3	9.63	1.194	8.436	88	1.681†	7.949	83	1.907†	7.723	80
Postfire 2c	3	7.77	1.231	6.540	84	0.900	6.870	88	1.115	6.655	86
					TDN						
Prefire	2	9.41	0.740	8.670	92	0.892	8.518	91	0.990	8.420	89
Windstorm	1	4.28	0.944	3.336	78	1.555	2.725	64	1.478	2.802	65
Postfire 1a	3	4.74◇	0.638	4.102	87	1.622†	3.118	65	1.822†	2.918	62
Postfire 1b	3	3.98◇	0.642	3.338	84	1.066	2.914	73	1.226	2.754	69
Postfire 2a	3	6.01†	1.079†	4.931	82	1.194†	4.816	80	1.288	4.722	79
Postfire 2b	3	8.66	1.057	7.603	88	1.493	7.167	83	1.748†	6.912	80
Postfire 2c	3	7.13	1.062	6.068	85	0.816	6.314	89	1.010	6.120	86
					Susp N						
Prefire	2	0.77	0.080	0.690	90	0.138	0.632	82	0.195	0.575	75
Windstorm	2	1.25	0.116	1.134	90	0.243	1.007	81	0.515	0.735	59
Postfire 1a	1	1.20	0.071	1.129	94	0.203†	0.997	83	0.228†	0.972	81
Postfire 1b	3	1.15†	0.071	1.079	94	0.128	1.022	89	0.145◇	1.005	87
Postfire 2a	3	1.43	0.062	1.368	96	0.195	1.235	86	0.093◇	1.337	94
Postfire 2b	3	0.97	0.137†	0.833	86	0.188†	0.782	81	0.159	0.811	84
Postfire 2c	3	0.64	0.097	0.543	85	0.083◇	0.557	87	0.105◇	0.535	84

[a] In the NW subbasin, fire did not occur until period 2a and the statistical comparisons are based on a prefire period of 1971–80.

increased 15-fold. Effects were short-lived, with a return to near-normal exports in 1983–86 (Table 2). In the E subbasin, fire caused a striking increase in annual nitrate export. Exports peaked in 1975 at 550 g N·ha^{-1}·yr^{-1} (over 7 times background), 1 yr after the first fire, and did not return to prefire levels before the second fire (Table 2). The second fire caused a smaller increase in export in 1980–83 and levels remained higher than background until the 1986–88 period. The windstorm in 1973 also increased NO_3^- export in both E and NE subbasins as reported by Schindler et al. (1980).

Nitrate export in the NE subbasin doubled after the first fire in 1974 and increased slightly after the 1980 fire. Nitrate export was 10-fold lower after both fires in this peatland subbasin than in the two terrestrial subbasins (Table 2).

Ammonium exports from the NW subbasin were low (15–50 g N·ha^{-1}·yr^{-1}) before the fire. However, ammonium exports were equally elevated after fire (1980–83), windstorm (1973–74), and the 1983–86 period (Table 2). Exports from the NE subbasin were higher after the first fire, with peaks in 1974–75 and 1977 at 150–180 g N·ha^{-1}·yr^{-1} (2 times prefire). There was no apparent effect of the second fire compared with the prefire period. Exports were elevated in the 1983–86 period. Exports of ammonium from the E subbasin increased more after the windstorm and in the 1983–86 period than during the two periods immediately postfire (Table 2).

The annual export of TDN increased significantly in the NE and E subbasins after the 1974 fire (Table 2). After the 1980 fire, TDN was significantly higher than prefire exports in the E subbasin but not in the boggy NE subbasin. After the first fire in the NW subbasin, there was a significant increase in TDN export.

The annual export of total nitrogen (TN) and Susp N increased significantly in the NE and E subbasins after the 1974 fire (Table 2). After the second fire (1980), the E subbasin showed a significant increase in TN, but the boggy NE subbasin did not show an increase. The NW subbasin showed a significant increase in export of TN after the 1980 fire that was due primarily to the increased export of TDN.

Annual retention of all N forms was high in all subbasins regardless of fire or windstorm (Table 2). Nitrate retention was generally greater than 90% of inputs except for just after the 1974 fire in the E subbasin. In the NW subbasin, percent retention ranged from 80 to 92% of all N inputs regardless of fire. The greatest export (or lowest percent retention) was observed for TDN in the E and NE subbasins after both windstorm and fire. The second fire did not decrease percent retention in either the E or NE subbasin.

Percent retention of N was higher than percent retention of P in both wetland and upland subbasins. In the wetland, net TN retention averaged 77% of deposition versus 80 and 87% for the E and NW upland subbasins for the entire 18-yr period of record. The comparable retention of total phosphorus (TP) was 51% in the wetland subbasin versus 67 and 84% for the E and NW subbasins, respectively. Presumably more N is retained than P because these boreal forest ecosystems are N limited. There was no significant difference between the subbasins due to the wide variance caused by the fire events.

The annual export of TDP and TP increased in the NE subbasin after the first burn (1974) (Table 3), with the peak loss of TDP and TP in 1975 at 152 and 183 g·ha^{-1}·yr^{-1}, respectively. There was no significant increase in export of TDP or TP from the E subbasin after the 1974 fire. There was no increase in Susp P export from any subbasin (data not shown). The 1980 fire had no effect on P export from any subbasin. Percent retention of TP and TDP was lower after fire in the NE subbasin than in the upland subbasins.

Changes in Mean Annual Stream Concentrations after Fire

Nitrate

The first burning affected both upland subbasin streams similarly. In the E subbasin stream, the 1974 fire caused the mean annual concentration of NO_3^- to increase from 22 to 173 μg·L^{-1}. In the 3 yr after the fire, there was an average sixfold increase over the prefire concentrations. The second (1980) burning of the E subbasin did not cause an effect of similar magnitude, although concentrations had not returned to levels observed in 1971–73 before the fire occurred (Fig. 3A). In the 3 yr after the first fire (1980) in the NW subbasin, stream concentrations of NO_3^- increased sixfold compared with the prefire period (1971–80) (161 versus 24.6 μg·L^{-1}) (Table 4).

In the wetland stream (NE), NO_3^- concentrations increased after both fires compared with the prefire period, but the concentrations were much lower than in the terrestrial basins (Table 4).

Ammonium

After the first fire (1974), NH_4^+ concentrations increased rapidly in both the E and NE subbasin streams, peaking 3 yr later in 1977 (Fig. 3B). Values after that time remained above the 1971–73 value, but were little affected by the 1980 burn (Table 4).

TABLE 3. Input, export, and retention of TDP and TP in the three ELA watersheds before and after fire (data in kg·ha^{-1}·yr^{-1}). %R = % retention. The symbol † denotes data significantly higher ($p > 0.95$) and ◇ denotes data significantly lower than the prefire period (June 1971 to June 1973) in the NE and E subbasins. Double underline denotes when the first fire occurred.

Period	No. of years	Input	NW[a]			E			NE		
			Export	Retention	%R	Export	Retention	%R	Export	Retention	%R
						TDP					
Prefire	2	0.41	0.023	0.387	94	0.032	0.378	92	0.039	0.371	90
Windstorm	1	0.12	0.022	0.098	82	0.050	0.070	58	0.060	0.060	50
Postfire 1a	3	0.10◇	0.012	0.088	88	0.039	0.061	61	0.103†	−0.003	−3
Postfire 1b	3	0.07◇	0.010	0.060	86	0.028	0.042	60	0.040	0.030	43
Postfire 2a	3	0.10◇	0.019	0.081	81	0.038	0.062	62	0.039	0.061	61
Postfire 2b	3	0.10◇	0.026	0.074	74	0.038	0.062	62	0.037	0.063	63
Postfire 2c	3	0.06	0.010◇	0.050	83	0.015◇	0.045	75	0.021◇	0.041	68
						TP					
Prefire	2	0.58	0.032	0.548	95	0.050	0.530	91	0.060	0.520	90
Windstorm	1	0.25	0.033	0.277	87	0.080	0.170	68	0.125	0.125	50
Postfire 1a	3	0.24◇	0.017	0.223	93	0.061	0.179	75	0.126†	0.114	48
Postfire 1b	3	0.21◇	0.015	0.195	93	0.042	0.168	80	0.053	0.157	75
Postfire 2a	3	0.29◇	0.027	0.263	91	0.065	0.225	78	0.048◇	0.242	83
Postfire 2b	3	0.20◇	0.039	0.161	81	0.059	0.141	71	0.054	0.416	73
Postfire 2c	3	0.12	0.025	0.095	79	0.024◇	0.096	80	0.032◇	0.088	73

[a] In the NW subbasin, fire did not occur until period 2a and the statistical comparisons are based on a prefire period of 1971–80.

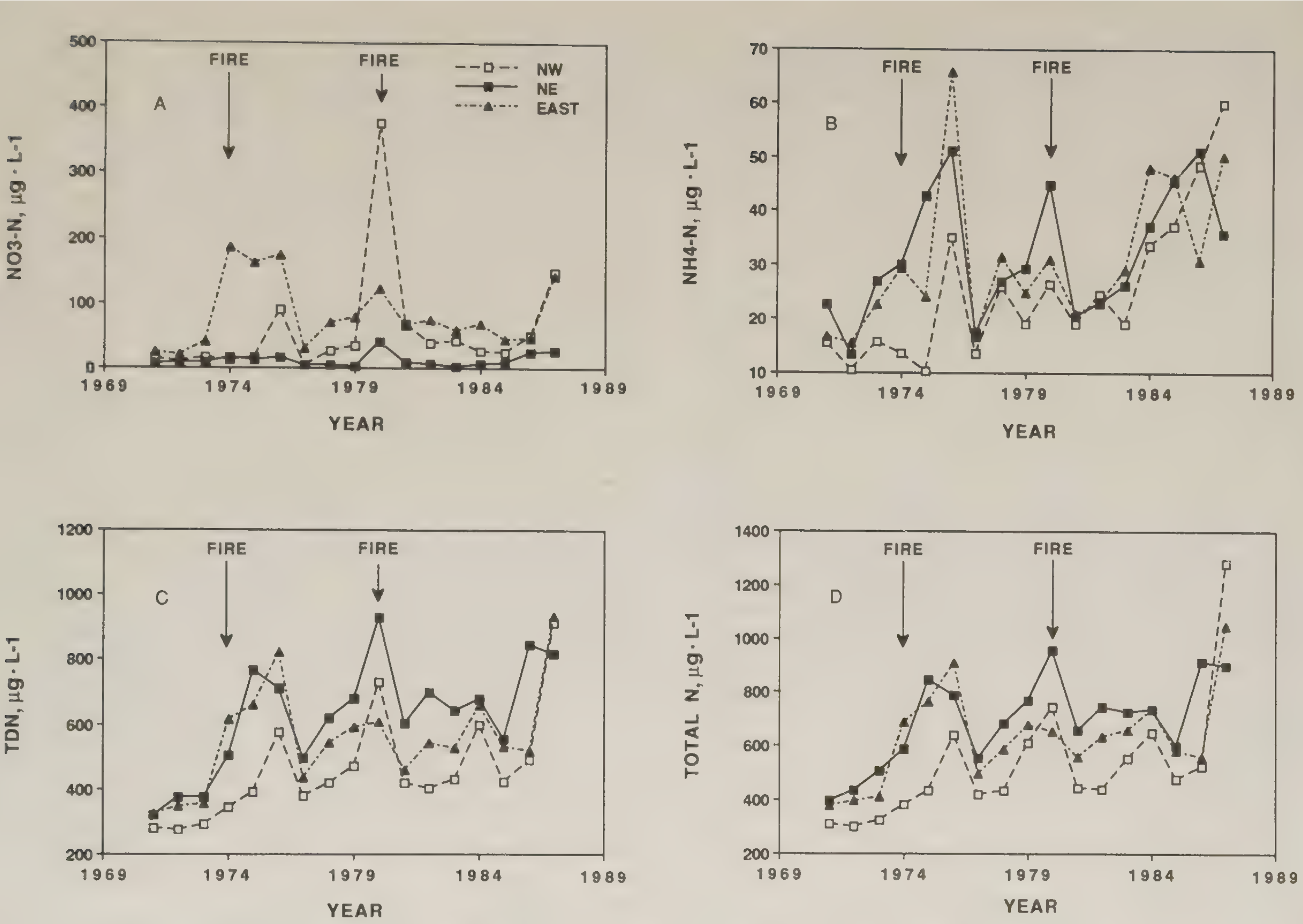


FIG. 3. Mean annual concentration of N species in the three ELA streams from 1971 to 1989.

TABLE 4. Concentrations of N in streamwater from three ELA watersheds before and after fire (data in $\mu g \cdot L^{-1}$). The symbol † denotes data significantly higher ($p > 0.95$) and ◇ denotes data significantly lower than the prefire period (June 1971 to June 1973) in the NE and E subbasins. Double underline denotes when the first fire occurred.

Period	No. of years	NO$_3^-$–N			NH$_4^+$–N			Susp N			TDN			TN		
		NW[a]	E	NE	NW[a]	E	NE	NW[a]	E	NE	NW[a]	E	NE	NW[a]	E	NE
Prefire	2	12.8	22.5	6.0	13.0	16.1	18.1	29.7	51.3	67.7	276.7	334.4	347.1	306.4	385.7	414.8
Windstorm	1	15.1	40.1	8.7	15.7	22.6	26.9	35.5	55.5	131.0	289.7	355.6	376.0	325.1	411.1	507.0
Postfire 1a	3	38.8	173.4†	14.4†	19.6	39.7†	41.3†	48.7	88.1†	80.9†	436.7	696.7†	659.1†	485.4	784.8†	740.0†
Postfire 1b	3	21.5	58.9†	2.8◇	19.5	24.3†	24.6†	64.1	64.2	72.4	424.2	522.4†	596.7†	488.2	586.6†	669.1†
Postfire 2a	3	161.1†	87.2†	18.2	23.5	25.0†	29.5†	26.8	80.0†	44.5◇	516.5	536.0†	742.4†	543.3	616.0†	787.0†
Postfire 2b	3	30.4	56.0†	5.8	30.1†	41.1†	36.4†	76.5†	87.0†	61.9	484.6	570.4†	625.1†	561.2	657.4†	687.0†
Postfire 2c	3	84.0†	96.3†	18.0†	40.3†	31.7†	34.3†	65.6†	75.0	77.3†	730.8†	720.2†	785.7†	890.7†	795.1†	863.2†

[a] In the NW subbasin, fire did not occur until period 2a and the statistical comparisons are based on a prefire period of 1971–80.

In the NW subbasin stream, there was little evidence that fire caused an increase in NH$_4^+$ concentrations after the 1980 fire (Table 4). Concentrations in all three basins increased in the dry periods (1984, 1986, and 1987). Drought in 1976 also caused an increase in NH$_4^+$ in the unburned NW subbasin (Fig. 3B).

Suspended nitrogen

In the NE stream, the concentration of Susp N increased significantly after the 1974 fire compared with the prefire conditions (Table 4). Postfire peaks were also observed in the E stream, but the peaks followed both fires by 2 yr. Susp N concentrations in the NW stream were fairly constant from 1971 to 1978 and were erratic thereafter without apparent cause (drought or fire).

Total dissolved nitrogen

TDN constituted about 66% of the TN lost from all three subbasin streams (Fig. 3C). The 1974 fire caused approximately a twofold increase in TDN in both the NE and E subbasin streams (Table 4). There is some evidence for a partial recovery in 1977, but the 1980 burn caused the TDN concentrations to remain high in both subbasins (Fig. 3C). In the NW stream, there was no significant effect of the fire on TDN concentrations based on the 3-yr fire period (Table 4), but during the fire year (1980), concentrations increased dramatically (Fig. 3C) and then returned to background levels within a year.

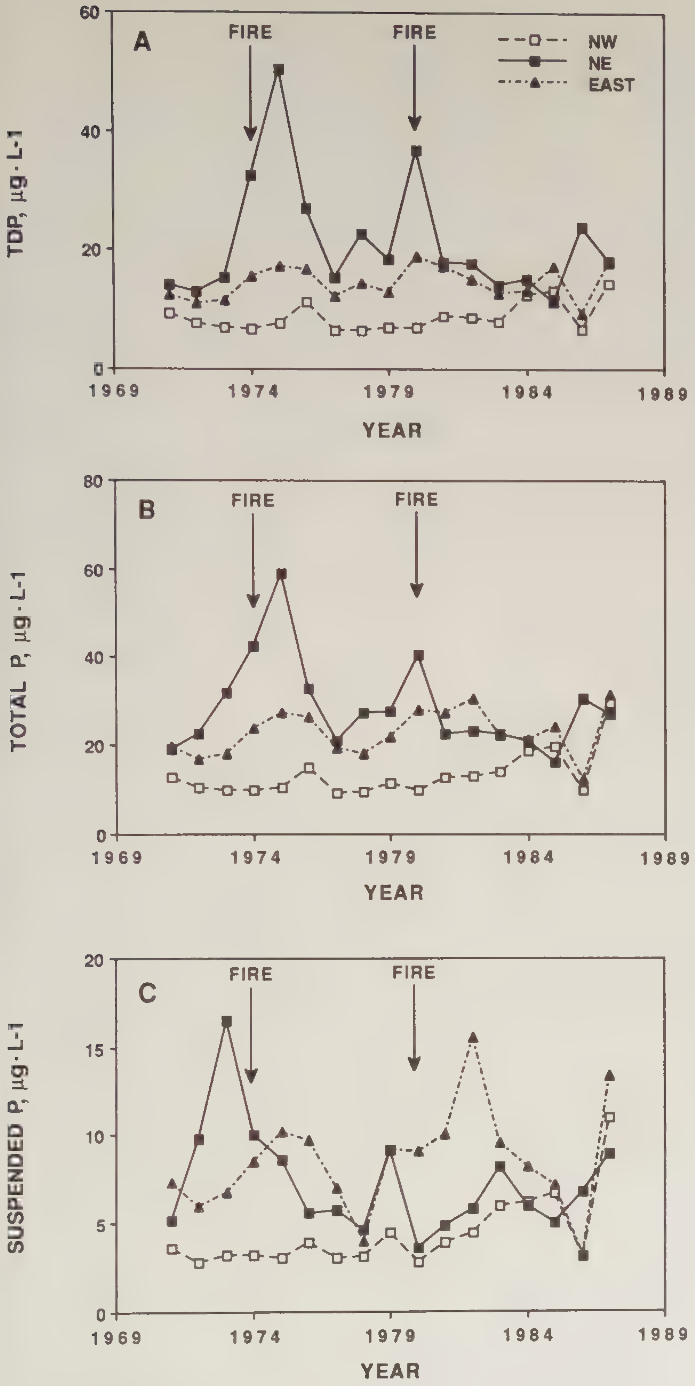


FIG. 4. Mean annual concentration of P in the three ELA streams from 1971 to 1989.

Concentrations in the NW stream in the period 1974–80 before the first fire were significantly higher than in 1971–73, presumably due to leaching of imported ash from fires in the adjacent subbasins (Fig. 3C).

Total nitrogen

TN concentrations largely mirrored patterns in TDN (Fig. 3D). Concentrations after the 1974 fire were doubled in both NE and E streams (Table 4) and remained higher than prefire values through 1979. After the second fire, concentrations of TN increased again in the NE stream, but not in the E stream. In the NW stream, concentrations of TN generally increased through the 1970's, with peaks in 1975 and 1979 (Fig. 3D). The fire in 1980 produced a significant increase in TN if the entire prefire record (1971–80) was compared with the 1980 fire year alone (429 versus 745 $\mu g \cdot L^{-1}$), but not if the fire period 1980–83 was used (543 $\mu g \cdot L^{-1}$ in Table 4). In 1979–88, all streams usually had high concentrations of TN and TDN, but the effects of drought and fire cannot be separated. In the 1976 drought, the unburned NW subbasin had elevated stream concentrations of both TDN and TN.

Total dissolved phosphorus and total phosphorus

Concentrations of TDP in the NW stream ranged from 6 to 10 $\mu g \cdot L^{-1}$, with no apparent impact of the 1980 fire (Fig. 4A). In contrast, both fires caused a 30% increase in the concentrations in the E stream. The wetland-dominated NE stream had dramatic increases (over 3 times in 1975) in concentration following the 1974 fire, although the second fire caused increased concentrations only for 1 yr, not the entire 1980–83 period (Table 5). The pattern of TP concentrations in the three streams (Fig. 4B) was similar to those described for TDP, with the wetland stream showing the largest response to fire.

Suspended phosphorus

While more variable than TDP, Susp P concentrations in the NW stream were similar, showing no effect of fire (Fig. 4C). However, concentrations increased during the 1983–88 period, but this increase cannot be attributed to fire during this very dry period. In the E stream, concentrations increased after both fires (Table 5). The windstorm but not the fire increased Susp P in the NE stream (Fig. 4C). There was no detectable increase in Susp P after the 1980 fire in the NE subbasin.

Effect of Fire on Monthly Concentrations and Flows

Nitrate

The greatest effect of fire on NO_3^- concentration in all streams was during the nonvegetative season with increased concentrations and high variability (Fig. 5; only NW stream shown). During summer months, growing vegetation took up NO_3^- so that stream concentrations did not differ significantly from preburn years.

Ammonium and suspended nitrogen

The pattern for NH_4^+ in the E stream was similar to that for NO_3^- in the NW stream, with postfire concentrations above prefire values during early spring and fall, but relatively unchanged during the vegetative season. An exception was the NW subbasin, where postfire values were not significantly different from prefire values (Fig. 6). There was little evidence of postfire changes in Susp N. Values exceeded the normal prefire range only in a few incidental samples collected in midwinter in the NE stream (data not shown).

Total dissolved nitrogen

In both upland (E) and wetland (NE) subbasins, concentrations of TDN were much higher throughout the year after fire, with little evidence of a seasonal pattern (Fig. 7A; NE data not shown). In contrast, the seasonal pattern for TDN in the NW stream following the 1980 fire showed a pronounced spring maximum and summer minimum, similar to NO_3^- concentrations (Fig. 7B).

Total dissolved phosphorus

Evidence for seasonally elevated concentrations of TDP due to fire was observed only in the NE stream. The increase was most pronounced in winter (5 times), dropping to less than 2 times for the remainder of the year (Fig. 8).

TABLE 5. Concentrations of Susp P, TDP, and TP in the three ELA streams before and after fire (data in $\mu g \cdot L^{-1}$). The symbol † denotes data significantly higher ($p > 0.95$) and ◇ denotes data significantly lower than the prefire period (June 1971 to June 1973) in the NE and E subbasins. Double underline denotes when the first fire occurred.

Period	No. of years	Susp P			TDP			TP		
		NW[a]	E	NE	NW[a]	E	NE	NW[a]	E	NE
Prefire	2	3.2	6.6	7.5	8.5	11.7	13.4	11.7	18.4	20.9
Windstorm	1	3.2	6.8	16.5	6.9	11.5	15.3	10.0	18.3	31.9
Postfire 1a	3	3.4	$9.5^{\dagger}$	8.1	8.5	$16.5^{\dagger}$	$36.6^{\dagger}$	11.9	$26.0^{\dagger}$	$44.7^{\dagger}$
Postfire 1b	3	3.5	6.7	6.5	6.6	$13.1^{\dagger}$	$18.9^{\dagger}$	10.1	$19.9^{\dagger}$	$25.4^{\dagger}$
Postfire 2a	3	3.7	$11.5^{\dagger}$	$4.8^{\diamond}$	8.2	$17.0^{\dagger}$	$24.1^{\dagger}$	12.0	$28.6^{\dagger}$	$28.9^{\dagger}$
Postfire 2b	3	$6.3^{\dagger}$	$8.3^{\dagger}$	6.4	$11.2^{\dagger}$	$14.3^{\dagger}$	13.4	$17.5^{\dagger}$	$22.7^{\dagger}$	19.9
Postfire 2c	3	$7.1^{\dagger}$	$8.3^{\dagger}$	7.8	10.3	13.3	$17.9^{\dagger}$	$18.9^{\dagger}$	21.5	$25.9^{\dagger}$

[a] In the NW subbasin, fire did not occur until period 2a and the statistical comparisons are based on a prefire period of 1971–80.

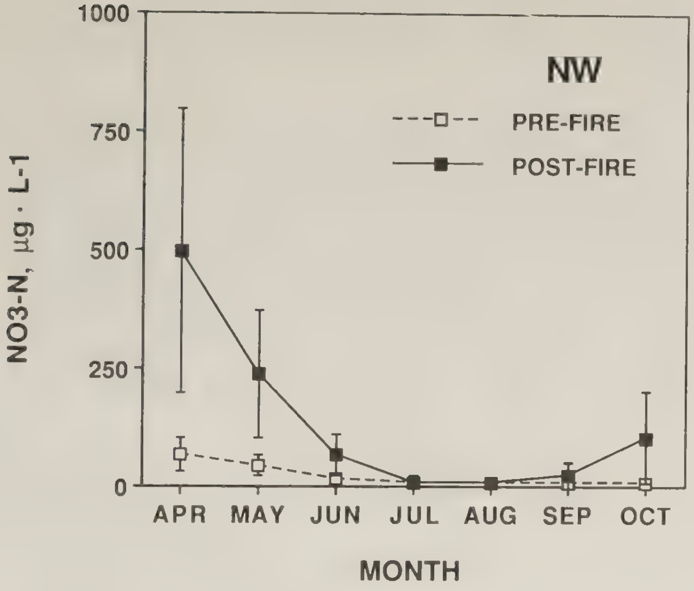


FIG. 5. Monthly concentrations of NO_3^--N before and after fire in the NW stream (mean ± 2 SE).

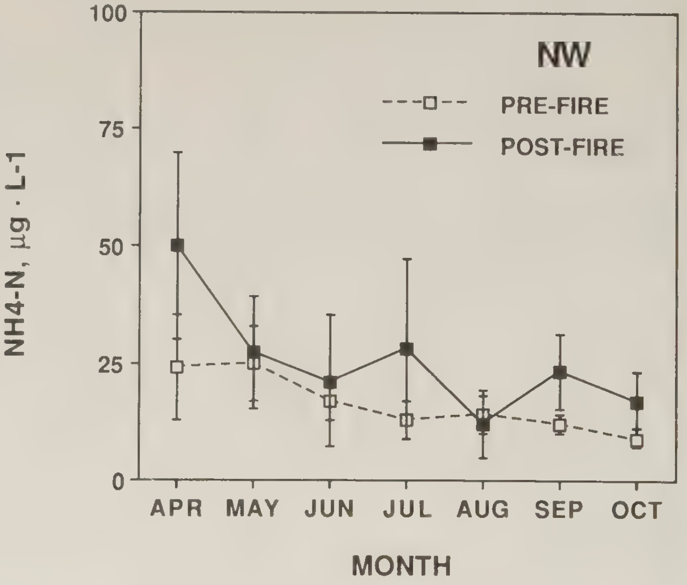


FIG. 6. Monthly concentrations of NH_4^+-N before and after fire in the NW stream (mean ± 2 SE).

Nitrogen and Phosphorus Budgets of Lake 239

Fire in the subbasins of L239 increased the inputs of TN to the lake. However, fire was not an important contributor because TN inputs from precipitation ranged from 36 to 59% of the total inputs and were independent of the fires. The most striking feature of the long-term data set is the decrease in outflow of N over the 18-yr record (Table 6). In the 1980's, a greater proportion of the N entering the lake has been retained, and Schindler et al. (1990) attributed this to the decrease in the flushing time of the lake caused by the decreased precipitation and increased temperature during this period. Net retention of TN ranged from 54% of inputs in the year of the windstorm to 88% of inputs in the dry 1983–86 period. TP patterns of input and outflow in L239 are similar to those of TN (Table 6), with inputs of TP from runoff 38–65% of total inputs to the lake. TP export from the lake decreased over the period of record due to the decrease in the flushing rate of the lake. Fires in the three main subbasins of the lake were not as important to the nutrient budgets as the changes in precipitation, runoff volumes, and flushing rate during that period.

Discussion

Net Retention and Loss of Nutrients from Upland Watersheds

In the past, some fear has been expressed that nutrient losses from fires would be high enough to hinder the regrowth of new vegetation. This seems unlikely in the forested watersheds at ELA, given the small increases and relatively short period of elevated losses following a fire. In the NW subbasin, annual stream losses of N after the fire were only 15% of atmospheric input, compared with 12% before fire (Table 2). In the E subbasin the losses of N after the first fire were greater; 31% of annual atmospheric inputs were lost compared with 10% before fire. P losses were not great, with net losses after fire only slightly higher than prefire losses in the NW subbasin. In the E subbasin, a maximum of 39% of annual atmospheric P inputs were lost in the 1974 fire.

Upland areas retained most of the N and P entering with precipitation, even after two burns. It is probable that the fire actually increased the N available for forest growth, for concentrations of NH_4^+ in soil water of the E subbasin after the 1974 burn were a 1000-fold higher than concentrations in the unburned NW subbasin (D. W. Schindler, unpubl. data).

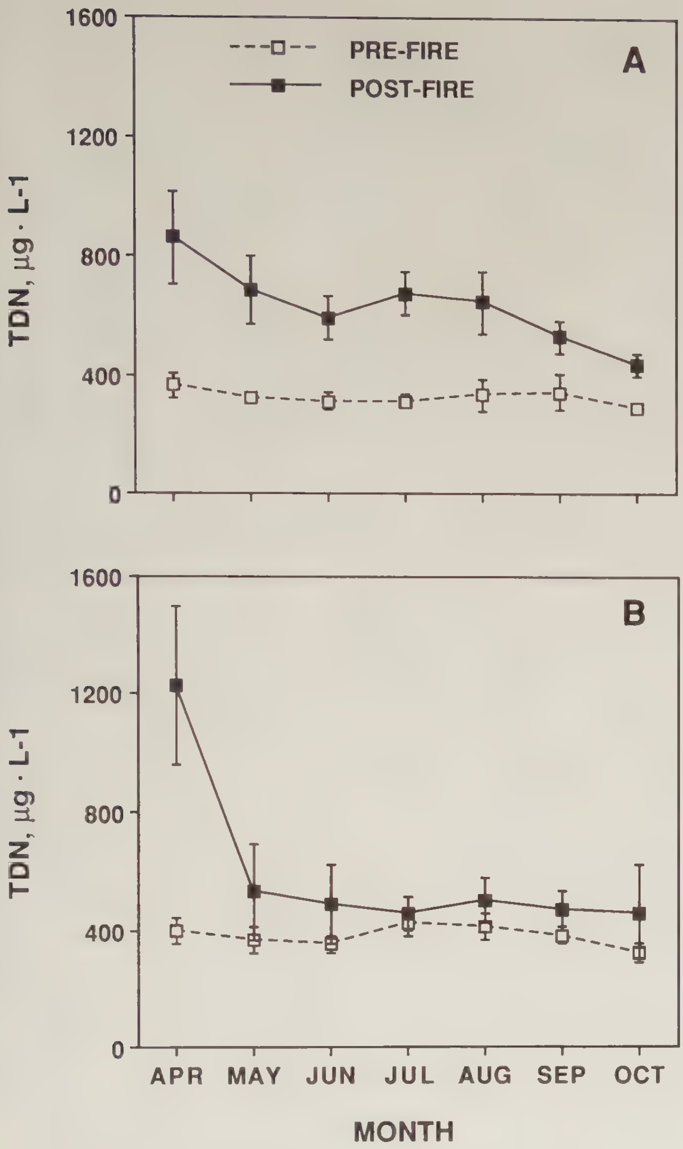


FIG. 7. Monthly concentrations of TDN before and after fire in the (A) NW stream and (B) E stream.

During the period of active plant growth, concentrations of NO_3^- in outflow were lower than in early spring and late fall, as one might expect (Fig. 5). This biological regulation was intense enough to prevent NO_3^- losses from exceeding the prefire confidence limits in the summer. During spring and fall when vegetation was dormant, the effect of fire was evident. In contrast, the NH_4^+ and TDN (which was primarily organic N) in the NW stream showed little evidence of a seasonal pattern, indicating that it was reasonably unaffected by vegetative uptake (Fig. 7).

Net Retention and Loss of Nutrients from the Wetland Watershed

Exports of P from the wetland (NE) subbasin were higher than from the upland areas, both before and after burning (Table 3). In the 3 yr after the 1974 fire, outflow losses were over half of the TP and all of the TDP supplied annually by precipitation. Net retention of TDP continued to be low until 6 yr after the second fire. After that time, over 60% of the TDP was retained. Net retention of TP (and Susp P) was higher than TDP and increased after the 1974–77 fire period so that net retention was generally greater than 70%. Retention of TP in the ELA wetland was higher than the retention measured by Devito et al. (1989) in eastern Canadian wetlands and was similar to values obtained by Verry and Timmons (1982) in Minnesota wetlands.

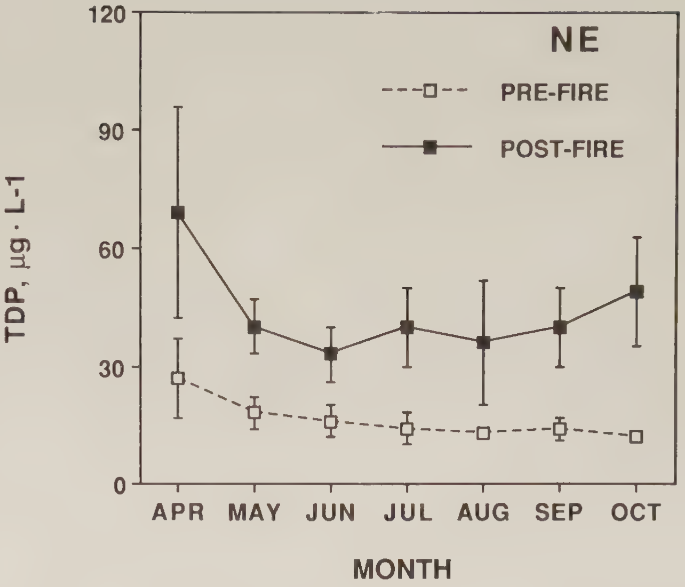


FIG. 8. Monthly concentrations of TDP in the NE stream before and after fire (mean ± 2 SE).

Exports of TN, TDN, and Susp N from the wetland subbasin (NE) were higher than exports from the terrestrial (E) subbasin for the comparable fire periods. This is expected because wetlands are known to export organic forms and retain inorganic forms of N (Devito et al. 1989). However, retention of TN by the wetland at ELA, even with the fire, was greater than 77% of inputs. This is also much higher than the net retention in eastern Canadian wetlands (Devito et al. 1989). NO_3^- export from the wetland subbasin was 7 times lower than from the upland subbasin. The low export of NO_3^- was expected because retention experiments with *Sphagnum* have shown NO_3^- assimilation to be extremely high (Bayley et al. 1987; Urban et al. 1988). NH_4^+ exports were sometimes higher from the wetland and sometimes higher from the terrestrial subbasins.

Effect of Multiple Fires and Fire Intensity on Nutrient Concentrations

A second fire in the basin within such a short time period might be expected to aggravate soil loss, increase erosion, and cause nutrient shortages for the vegetation. Such results were not investigated, although the terrestrial and wetland subbasins differed in behavior in terms of nutrient retention. While the first fire in the NE and E subbasins caused increased concentrations of N and P in those streams, recovery of P generally occurred within 2–3 yr after the first fire (Fig. 4). After the second fire, TP concentrations in the terrestrial E subbasin increased again and did not return to prefire levels. In the wetland subbasin (NE), the second fire did not cause an increased loss of P.

The elevated N concentrations (particularly TDN) in the streams were more prolonged than P. Baseline conditions in the NE and E streams had still not been reached by the time of the 1980 fire (Fig. 3C and 3D) and remained elevated through

TABLE 6. N and P budgets of L239 on an annual basis during periods before and after fire in the watershed (data in kg·ha^{-1}·yr^{-1}). %R = % retention.

Period	No. of years	Export from terrestrial areas to lake NW	EAST	NE	Direct runoff	Total runoff	Precipitation input	Total input	Output	%R
TN										
Prefire	2	0.974	1.169	1.414	1.217	1.160	9.915	17.152	5.632	67
Windstorm	1	0.673	1.037	1.155	1.046	0.984	5.410	11.554	5.338	54
Postfire 1a	3	0.691	1.754	1.908	1.735	1.577	5.337	15.187	6.023	60
Postfire 1b	3	0.836	1.478	1.755	1.510	1.391	5.890	14.579	5.433	63
Postfire 2a	3	1.082	1.360	1.374	1.349	1.311	5.950	14.137	4.245	70
Postfire 2b	3	1.137	1.548	1.815	1.589	1.501	10.100	19.479	2.274	88
Postfire 2c	3	0.932	0.739	0.951	0.883	0.822	7.937	13.437	2.334	82
TP										
Prefire	2	0.050	0.062	0.082	0.066	0.062	0.530	0.916	0.204	78
Windstorm	1	0.019	0.041	0.049	0.042	0.038	0.380	0.615	0.129	79
Postfire 1a	3	0.020	0.066	0.135	0.080	0.065	0.220	0.626	0.131	79
Postfire 1b	3	0.019	0.049	0.069	0.052	0.046	0.247	0.531	0.115	78
Postfire 2a	3	0.023	0.062	0.047	0.056	0.053	0.207	0.539	0.100	82
Postfire 2b	3	0.035	0.050	0.051	0.050	0.047	0.263	0.559	0.102	82
Postfire 2c	3	0.026	0.033	0.030	0.032	0.031	0.123	0.318	0.058	82
Areas of basins (ha)		56.38	170.28	12.43	99.97	339.06	54.28	54.28	54.28	

1988. While the 1980 fire caused new increases in concentration of N and P, the relative increase was weaker than after the 1974 fire. The TDN concentrations in 1986–89 were higher in all three subbasins than during any other period in the 18-yr record (Table 4). This 3-yr period was also a very dry period (Table 1).

Both fires in the E subbasin were much more intense than the one in the NW. In the former basin, almost all organic matter was completely consumed whereas in the NW subbasin, most vegetation was killed by the fire, but little organic matter was oxidized and even the dead needles on coniferous trees were left intact. It is likely that the more intense fire consumed more organic matter which in turn made more N and P available to be leached. This difference may explain why increased losses of N and P occurred for several years after the E subbasin burned, but not in the NW where increased losses of NO_3^- and TDN occurred only in 1980 fire year but not in subsequent years.

TABLE 7. Comparison of ELA subbasin outflow altered by fire and by clearcutting (data in µg·L^{-1}).

	Clearcut subbasins[a]			East subbasin		
	Uncut	After 1 yr	After 2 yr	1971–73 (prefire)	1975 (after 1 yr)	1976 (after 2 yr)
NO_3^-	40	20	10	28	193	194
NH_4^+	10	60	20	15	25	34
TDN	480	790	560	330	660	720
Susp N	40	70	50	53	81	120
TDP	10	30	10	12	18	19
Susp P	3	8	4	6	11	11

[a] Data from Nicolson (1975) (no standard error given). Data are from weekly samples collected during the 1973 growing season and analysed by the Freshwater Institute laboratory. The subbasins included three uncut subbasins, two subbasins cut 1 yr previously, and three subbasins cut 2 yr previously.

Changes in the Nutrient Budget of Lake 239

The total inputs of P and N to the lake were only slightly affected by fire. Approximately half of the input of both nutrients was by direct precipitation on the lake surface, and this was unaffected by the fire. Runoff of TP to the lake from the entire watershed increased by only 5%, while the TN exported to the lake from the entire watershed increased by 26% in the 3 yr after the fire (Table 2). Given that the long-term water renewal time for L239 is 9.1 yr and that inputs (particularly of P) would be elevated for much less than that period, it is unlikely that nutrient concentrations, productivity, or phytoplankton standing crop of the lake would increase due only to fire. Schindler et al. (1990) did observe increases in N concentration, productivity, and phytoplankton biomass in the 18-yr period, but decreased precipitation and increased water renewal times of L239 cannot be separated from the influence of fire on lake nutrient chemistry.

It seems reasonable to conclude that forest fires in the ELA region have minimal effect on the quality of any lakes with water renewal times long enough to minimize the effect of a few years of slightly elevated nutrient input. Because most Precambrian Shield lakes are P limited (Schindler 1977), the relatively small (average 2 times) and short duration (2–3 yr) of increased P losses from upland watersheds makes it unlikely that a fire would cause eutrophication of larger lakes. However, in small streams and rapidly flushed lakes, eutrophication could occur for several years following fire. The highest likelihood of eutrophication in lakes would be in situations where catchments with high proportions of wetlands were burned, and where these drained to lakes with high rates of water renewal, i.e. where new, higher steady-state nutrient concentrations

TABLE 8. Comparison of chemical concentrations in outflow from forested watersheds after fire or clearcutting. The upper number is the baseline concentration; the number in parentheses is the concentration after the fire or disturbance. % + denotes percent increase.

	E subbasin[a]	% +	Hubbard Brook[b]	% +	Coweeta[c]	% +	Andrews[d]	% +
NO_3^-	28.3		212.0		5.5		≈3.0	
	(141.3)	500	(11973.0)	5627	(91.0)	1655	(62.0)	2067
NH_4^+	14.9		109.0		4.0		4.0	
	(32.1)	215	(39.0)	0	(4.5)	≈0	(3.0)	≈0

[a] ELA (this study).
[b] Bormann et al. (1968, 1974) and Likens et al. (1969, 1970).
[c] Swank and Douglass (1977).
[d] Dahm (1980).

could be reached in a short time. Due to prolonged increases in N, increasing ratios of N:P might be expected following fire, as shown by Schindler et al. (1991). Such changes might cause eutrophication of N-limited lakes and are correlated with increases in phytoplankton diversity in L239.

Effects of Fire versus Clearcutting on Stream Chemistry at ELA

Effects of clearcutting on chemical concentrations in boreal streams at ELA were studied by Nicolson in the early 1970's and are summarized in Nicolson (1975). Both fire and clearcutting increased the concentrations of most ions exported in the outflow of ELA subbasins. The increased concentrations following fire appeared to last longer than the effects due to clearcutting, although Nicolson's study included only 2 yr after clearcutting. In the first year after clearcutting, Nicolson (1975) found that concentrations of seven ions in streams from a clearcut area were significantly different from undisturbed subbasins (Table 7). Most of the ions were significantly higher in the streams from clearcut areas, but NO_3^- concentrations were significantly *lower* than in the undisturbed basins.

NO_3^- concentrations in streams were lower in the clearcut basins (10–20 $\mu g \cdot L^{-1}$) than from undisturbed basins (40 $\mu g \cdot L^{-1}$). After fire, NO_3^--N concentrations were higher (193 $\mu g \cdot L^{-1}$) than in undisturbed basins (Tables 4 and 8). The reasons for the decline in NO_3^- after clearcutting at ELA detected by Nicolson (1975) are not known, although high NO_3^- uptake by the remaining vegetation, slow rates of remineralization of slash and detritus, and the very low N concentration of soil organic matter and vegetation could contribute. Nicolson's finding is contrary to most other watershed studies of clearcutting (Bormann et al. 1968, Likens et al. 1969, 1970; Aubertin and Patric 1974; Swank and Douglass 1977; Dahm 1980; Swank and Caskey 1982).

Comparisons of Nitrogen Concentrations in Streams Draining Perturbed Forested Ecosystems

Increases in NH_4^+ concentrations after burning in the E and NE subbasins (Fig. 3B) and from clearcutting at ELA (Table 8) contrast with the effects of clearcutting in other regions where no increases in NH_4^+ were detected (Bormann et al. 1968; Likens et al. 1970; Aubertin and Patric 1974; Swank and Douglass 1977; Dahm 1980). The increase in NH_4^+ was very large for some weeks after the 1974 fire. The short-term increase in NH_4^+ may be due to the intensity of the burn, which remineralized the forest vegetation and organic matter in soil. Leaching experiments in soil columns from the E subbasin just after the 1974 fire revealed that most of the water-leachable N was present as NH_4^+ (D. W. Schindler and G. Morrison, unpubl. data). Nonetheless, most of the inorganic N leaving the watershed was NO_3^- (Fig. 3A and 3B). This presumably resulted from nitrification, as was found at Hubbard Brook following clearcutting (Likens et al. 1969; Bormann et al. 1974).

Concentrations of NO_3^- exported from unmodified ELA subbasins were lower than baseline concentrations from Hubbard Brook (Likens et al. 1970) but higher than most values from Coweeta Basin and H. J. Andrews Experimental Forest (Table 8) (Swank and Douglass 1977; Dahm 1980). Postfire concentrations of NO_3^- were higher than clearcutting effects at Coweeta Basin or H. J. Andrews Forest but not as high as the effects of clearcutting plus herbicide at Hubbard Brook. Wright (1976) did not detect increases in NO_3^- in streams from burned forests located only 300 km south of ELA, although he did not start sampling until 1 yr after the fire event. Since we detected only temporary increases (<1 yr) in NO_3^- concentrations after the fire in the NW basin and more persistent increases in concentration in the E stream, it is apparent that increases in NO_3^- concentration are not a consistent result of either fire or clearcutting in boreal watersheds. Vitousek et al. (1979) also found that N-poor forest ecosystems did not leach NO_3^-, as was observed in streams from a more nutrient-rich temperate forest.

Summary

The first wildfire in the wetland watershed (NE) increased water yields and mass export of NO_3^-, NH_4^+, TDN, Susp N, TN, TDP, and TP compared with the prefire levels. In the upland watershed (E), water yields and mass export of NO_3^-, NH_4^+, TDN, Susp N, and TN increased, while export of TDP and TP did not. Concentrations of all forms of N and P in stream water also increased after the first fire in the E subbasin. In general, N losses partially recovered 5–6 yr after the fire, while P losses returned to normal 2–3 yr after the fire.

A second fire in 1980 reburned the E and NE subbasins and burned the NW subbasin for the first time. Weaker, but distinct, increases in NH_4^+ and TDN were noted in the wetland outflow and in NO_3^-, Susp N, TDP, and Susp P in the twice-burned upland stream. In the NW subbasin, which was first burned in 1980, there was no significant increase in the annual concentration of P for the 3 yr after the fire or in most forms of N. The lack of response in most forms of N and P fractions was probably due to the lower intensity of fire in the NW subbasin.

Fire caused changes in seasonal export patterns in NO_3^-, TDN, and TDP in all subbasins. In the case of TDN, a signif-

icant increase in concentration was noted throughout 1980 in all basins. For other chemical species, baseflow concentrations in early spring and late fall were elevated, while concentrations in midsummer were within the prefire range.

Acknowledgments

We thank G. Linsey and M. A. Turner for their assistance in the chemical analysis of samples and preparation of data and numerous field and laboratory staff who helped to collect, analyse, and maintain the 18-yr record of stream chemistry and hydrology at ELA. We also thank Sandi Vitt for the preparation of the manuscript. This study was funded by the Canadian Department of Fisheries and Oceans. The World Wildlife Fund and NSERC Strategic Grant No. 40628 provided support for analysis of the long-term data set.

References

Aubertin, G. M., and J. H. Patric. 1974. Water quality after clearcutting a small watershed in West Virginia. J. Environ. Qual. 3: 243–249.

Bayley, S. E., D. H. Vitt, R. W. Newbury, K. G. Beaty, R. S. Behr, and C. Miller. 1987. Experimental acidification of a *Sphagnum*-dominated peatland: first year results. Can. J. Fish Aquat. Sci. 44(Suppl. 1): 194–205.

Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. Science (Wash., DC) 159: 882–884.

Bormann, J. H., G. E. Likens, T. G. Siccama, R. S. Pierce, and J. S. Eaton. 1974. The effect of deforestation on ecosystem export and the steady-state conditions at Hubbard Brook. Ecol. Monogr. 44: 255–277.

Brown, G. W., A. R. Gahler, and R. B. Marston. 1973. Nutrient losses after clear-cut logging and slash burning in the Oregon Coast Range. Water Resour. Res. 9: 1450–1453.

Brunskill, G. J., and D. W. Schindler. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 139–155.

Clark, J. S. 1990. Fire and climate change during the last 750 years in northwestern Minnesota. Ecol. Monogr. 60: 135–159.

Dahm, C. N. 1980. Studies on the distribution and fates of dissolved organic carbon. Ph.D. dissertation, Oregon State University, Corvallis, OR. 145 p.

DeByle, N. V., and P. E. Packer. 1972. Plant nutrients and soil losses in overland flow from burned forest clearcuts, p. 296–305. *In* S. C. Crallany, T. G. McLaughlin, and W. D. Striffler [ed.] Watersheds in transition. American Water Resources Association, Urbana, IL.

Devito, K. V., P. J. Dillon, and B. D. Lazerte. 1989. Phosphorus and nitrogen retention in five Precambrian shield wetlands. Biogeochemistry 8: 185–204.

Feller, M. C., and J. P. Kimmims. 1984. Effects of clearcutting and slash burning on streamwater chemistry and watershed nutrient budgets in southwestern British Columbia. Water Resour. Res. 20: 29–40.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Q. Res. 3: 329–282.

Johnson, A. H. 1979. Estimating solute transport in streams from grab samples. Water Resour. Res. 15: 1224–1228.

Johnson, P. L., and W. T. Swank. 1973. Studies of cation budgets in the southern Appalachians on four experimental watersheds with contrasting vegetation. Ecology 54: 70–80.

Likens, G. E., F. H. Bormann, and N. M. Johnson. 1969. Nitrification: importance to nutrient losses from a cutover forested ecosystem. Science (Wash., DC) 163: 1205–1206.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed ecosystem. Ecol. Monogr. 40: 23–43.

McColl, J. G., and D. F. Grigal. 1975. Forest fire: effects on phosphorus movement to lakes. Science (Wash., DC) 188: 1109–1111.

1977. Nutrient changes following a forest wildfire in Minnesota: effects in watersheds with differing soils. Oikos 28: 105–112.

Megahan, W. F. 1983. Hydrological effects of clearcutting and wildfire on steep granitic slopes in Idaho. Water Res. 19: 811–819.

Nicolson, J. A. 1975. Water quality and clearcutting in a boreal forest ecosystem. Can. Hydrol. Symp. 75 Proc. NRCC No. 15195: 734–738.

Richter, D. D., and C. W. Ralston. 1982. Prescribed fire: effects on water quality and forest nutrient cycling. Science (Wash., DC) 215: 661–662.

Riekerk, H. 1983. Impacts of silvaculture on flatwoods runoff, water quality and nutrient budgets. Water Resour. Bull. 19: 73–79.

Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

Schindler, D. W., S. E. Bayley, P. J. Curtis, B. R. Parker, M. P. Stainton, and C. A. Kelly. 1991. Synchronization of the carbon, nitrogen and phosphorus cycles in precambrian shield lakes and their watersheds. Hydrobiologia. (In press)

Schindler, D. W., K. G. Beaty, E. J. Fee, D. R. Cruikshank, E. R. DeBruyn, D. L. Findlay, G. A. Linsey, J. A. Shearer, M. P. Stainton, and M. A. Turner. 1990. Effects of climatic warming on lakes of the central boreal forest. Science (Wash., DC) 250: 967–970.

Schindler, D. W., R. W. Newbury, K. G. Beaty, and P. Campbell. 1976. Natural water and chemical budgets for a small Precambrium lake basin in central Canada. J. Fish. Res. Board Can. 33: 2526–2543.

Schindler, D. W., R. W. Newbury, K. G. Beaty, J. Prokopowich, T. Ruszczynski, and J. A. Dalton. 1980. Effects of a windstorm and forest fire on chemical losses from forested watersheds and on the quality of receiving stream. Can. J. Fish. Aquat. Sci. 37: 328–334.

Smith, D. W., and T. D. James. 1978. Characteristics of prescribed burns and resultant short-term environmental changes in *Populus tremuloides* woodland in southern Ontario. Can. J. Bot. 56: 1782–1791.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of fresh water. Fish. Environ. Can. Freshwater Inst. (Winnipeg, Man.) Spec. Publ. No. 25.

Swain, A. M. 1973. A history of fire and vegetation in northeastern Minnesota as recorded in lake sediments. Q. Res. 3: 383–396.

Swank, W. T. 1987. Stream responses to disturbance, p. 339–357. *In* W. T. Swank and D. A. Crossley, Jr. [ed.] Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, NY.

Swank, W. T., and W. H. Caskey. 1982. Nitrate depletion in a second-order mountain stream. J. Environ. Qual. 11: 581–584.

Swank, W. T., and J. E. Douglass. 1977. Nutrient budgets for undisturbed and manipulated hardwood forest ecosystems in the mountains of North Carolina, p. 343–363. *In* D. L. Correll [ed.] Watershed research in eastern North America. Smithsonian Institution, Edgewater, MD.

Tiedemann, A. R., C. E. Conrad, J. H. Dieterich, J. W. Hornbeck, W. F. Megahan, L. A. Viereck, and D. D. Wade. 1979. Effects of fire on water. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. WO-10: 28 p.

Tiedemann, A. R., J. D. Helvey, and T. D. Anderson. 1978. Stream chemistry and watershed nutrient economy following wildfire and fertilization in eastern Washington. J. Environ. Qual. 7: 580–588.

Urban, M. B., S. J. Eisenreich, and S. E. Bayley. 1988. The relative importance of denitrification and nitrate assimilation in mid-continental bogs. Limnol. Oceanogr. 33: 1611–1617.

Verry, E. S., and D. R. Timmons. 1982. Waterborne nutrient flow through an upland peatland watershed in Minnesota. Ecology 63: 1456–1467.

Vitousek, P. M., J. R. Gosz, C. C. Gries, J. M. Melillo, W. A. Reiners, and R. L. Todd. 1979. Nitrate losses from disturbed ecosystems. Science (Wash., DC) 204: 469–474.

Vitt, D. H., and S. E. Bayley. 1984. The vegetation and water chemistry of four oligotrophic basin mires in northwestern Ontario. Can. J. Bot. 62: 1485–1500.

Wright, R. F. 1976. The impact of forest fire on the nutrient influxes to small lakes in northeastern Minnesota. Ecology 57: 649–663.

Selection of Factors Affecting the Presence of Brook Trout (*Salvelinus fontinalis*) in Adirondack Lakes: A Case Study

J. J. Beauchamp

Mathematical Sciences Section, Engineering Physics and Mathematics Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6367, USA

S. W. Christensen

Ecosystem Studies Section, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6036, USA

and E. P. Smith

Department of Statistics, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

Beauchamp, J. J., S. W. Christensen, and E. P. Smith. 1992. Selection of factors affecting the presence of brook trout (*Salvelinus fontinalis*) in Adirondack lakes: a case study. Can. J. Fish. Aquat. Sci. 49: 597–608.

We used multiple logistic regression techniques to develop models for estimating the probability of brook trout (*Salvelinus fontinalis*) presence/absence as a function of observable water chemistry variables and watershed characteristics. The data set consists of the Adirondack Lakes Survey Corporation data collected on 1469 lakes during 1984–87. Two models fitted to a randomly selected development subset of lakes, using two sets of candidate explanatory/predictor variables of particular interest, were compared on the basis of coefficient consistency and predictive ability. In addition to the usual maximum likelihood logistic regression results, we also applied collinearity and other associated diagnostics and variable-selection procedures designed specifically for the logistic regression model to arrive at parsimonious models. Both models correctly predicted fish presence in more than 85% of the model development set and more than 80% of the lakes in the verification data. For those variables appearing in both models, the signs of the estimated coefficients were the same and in agreement with expectation. The removal of influential observations, as indicated by the logistic regression diagnostics, caused all of the estimated coefficients to increase in absolute magnitude. This results in a model which is more sensitive to changes in the explanatory variables.

À l'aide de fonctions logistiques de régression multiple, les auteurs ont élaboré des modèles pour estimer la probabilité de la présence ou de l'absence d'ombles de fontaine (*Salvelinus fontinalis*) sous la forme d'une fonction des variables observables de la chimie de l'eau et des caractéristiques du bassin versant. Ils se sont servis des données recueillies dans 1 469 lacs des monts Adirondack, de 1984 à 1987, par l'Adirondack Lakes Survey Corporation. Les deux modèles ajustés à un sous-ensemble de lacs choisis au hasard à l'aide de deux ensembles de variables prédictives d'intérêt particulier ont fait l'objet d'une comparaison portant sur le niveau de la valeur de prévision et le coefficient de cohérence. En plus des résultats habituels de régression logistique de vraisemblance maximale, les auteurs ont appliqué la colinéarité et d'autres procédures connexes de sélection variable et de diagnostique conçues uniquement pour le modèle de régression logistique afin d'obtenir des modèles parsimonieux. Les deux modèles ont permis de prévoir la présence de poissons dans plus de 85 % des lacs avec l'ensemble des données utilisées pour l'élaboration des modèles, et dans plus de 80 % des lacs avec l'ensemble des données de vérification. Dans le cas des variables apparaissant dans les deux modèles, le signe des coefficients estimés était le même, comme prévu. L'élimination des observations influentes révélées par le diagnostique de régression logistique a entraîné une augmentation de la grandeur absolue de tous les coefficients estimés. On obtient ainsi un modèle plus sensible aux fluctuations des variables prédictives.

Received December 12, 1990
Accepted October 4, 1991
(JA841)

Reçu le 12 décembre 1990
Accepté le 4 octobre 1991

One of the primary goals of the National Acid Precipitation Assessment Program (NAPAP) was the development of fish response models that could be used to predict changes in fish species status as a result of changes in water chemistry (Baker et al. 1990a). A related goal of a study sponsored by the Adirondack Lakes Survey Corporation (ALSC) was to explain patterns of fish distribution in the Adirondack lakes of New York State (Baker et al. 1990b). Information useful for addressing both of these goals is available from ALSC data collected on 1469 Adirondack lakes during 1984–87 (Kretser et al. 1989). In particular, the data base contains information on the catch of various fish species, on water chemistry variables, and on selected watershed characteristics. A map of the Adirondack study region along with the watersheds is given in Fig. 1.

This paper focuses on how logistic regression can be used to relate the presence or absence of brook trout (*Salvelinus fontinalis*) (an important sport fish) to water chemistry variables and watershed characteristics. From the ALSC data base, presence or absence of brook trout (the dependent variable) in each lake was inferred from the catch or lack of catch of the species in the ALSC survey. The 41 explanatory variables listed in Table 1 were also selected, from the larger set of information recorded for each lake, as those most likely to influence brook trout distribution. These variables can be grouped into six basic categories: (1) acidification response variables, (2) baseline

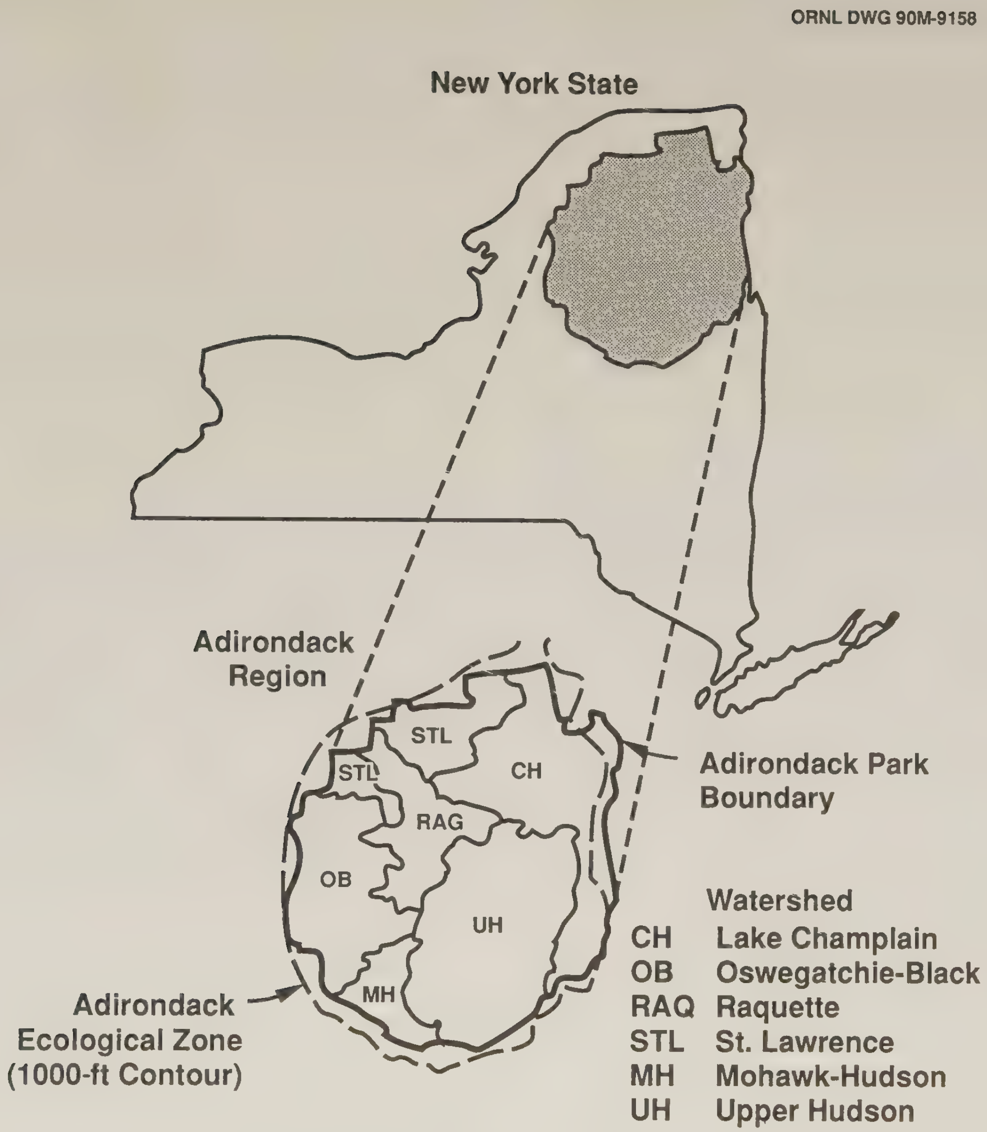


FIG. 1. Adirondack region showing both the Adirondack Park and Adirondack ecological zone boundaries (Source: Kretser et al. 1989).

habitat suitability variables, (3) productivity-related variables, (4) natural reproduction and access variables, (5) anthropogenic control variables, and (6) biological variables.

Developing models to describe the probability of presence/absence for a fish species from such survey data involves both difficulties and opportunities. The distribution and abundance of organisms is notoriously difficult to deal with because of the high variability associated with biological populations in general. In part, this variability reflects both the many influential factors and our inability to identify and/or measure many of these factors. Statistical problems such as choosing the wrong statistical model (model misspecification), errors in variables, and relationships among the explanatory variables (collinearities) are therefore to be expected. On the other hand, the fact that the ALSC used consistent sampling techniques to collect extensive information on a large number of lakes is encouraging. In particular, the data set is large enough to allow subdivision both for model development and model validation.

In addition to the usual maximum likelihood logistic regression results, we also applied collinearity and other associated diagnostics and variable-selection procedures designed specifically for the logistic regression model in order to arrive at a parsimonious model. The results of this paper demonstrate how available diagnostic tools for logistic regression can be used to (1) identify sets of explanatory variables that have a detrimental effect on parameter estimates because the variables are strongly collinear, (2) identify a parsimonious set of explanatory variables that may be used to predict or explain the presence of brook trout, and (3) identify potentially suspect data points. The results of this analysis can be useful in proposing possible cause–effect relationships between certain variables and the response variable (presence of fish) that can be tested in future studies. In this evaluation, we performed the analysis by using the ALSC data for brook trout. In order to evaluate the performance of the models, the data set was randomly divided into two parts (in an approximately 2:1 ratio): (1) a calibration data set used to derive the models and (2) a verification data set used to evaluate the selected models' predictive ability. Although other studies have investigated the development of empirical models to evaluate fish response to lake acidification (Reckhow et al. 1987), none of the existing papers appears to combine all of the aspects presented in this study (i.e. model formulation,

TABLE 1. List of candidate explanatory variables with transformation and summary of results from Mann–Whitney and contingency table analyses to test for differences between lakes with brook trout present versus absent for calibration data set.

Group number	Explanatory variable	Transformation[a]	χ_1^2[b]	P value
1	Acidification response variables			
	Field pH (standard units)	0	65.67(+)	<0.01
	Acid-neutralizing capacity (µeq/L)	L(150)	51.04(+)	<0.01
	Total aluminum (µg/L)	L(0)	41.03(−)	<0.01
	Estimated inorganic aluminum (µg/L)	L(1)	47.54(−)	<0.01
	Calcium (µeq/L)	L(0)	50.94(+)	<0.01
	Calcium + magnesium (µeq/L)	L(0)	51.89(+)	<0.01
	Sum of base cations (µeq/L)	L(0)	51.37(+)	<0.01
	Sodium (µeq/L)	L(0)	49.55(+)	<0.01
	pCa/pH	0	60.62(−)	<0.01
	Dissolved organic carbon (mg/L)	L(1)	6.65(−)	<0.01
	Flushing rate (times/year)	L(0)	7.44(−)	<0.01
2	Baseline habitat suitability variables			
	Minimum DO (mg/L)	0	2.21	0.14
	Maximum temperature (°C)	0	0.75	0.39
	Summer minimum temperature (°C)	0	4.12(−)	0.04
	Thermal stratification (1 = yes, 0 = no)	0	4.26(+)	0.04
	Maximum depth (m)	L(0)	12.39(+)	<0.01
	Elevation (m)	0	1.70	0.19
	Full bog (1 = yes, 0 = no)	0	5.87(−)	0.02
	Full bog or marginal bog (1 = yes, 0 = no)	0	6.81(−)	<0.01
	Beaver influence (1 = yes, 0 = no)	0	0.37	0.54
3	Productivity related variables			
	Total phosphorus (mg/L)	L(0.001)	3.76(−)	0.05
	Conductivity (H^+ adjusted)(µS/cm)	L(25)	43.07(+)	<0.01
	Area (ha)	L(0)	19.02(+)	<0.01
	Volume (m^3)	L(0)	27.05(+)	<0.01
	Mean depth (m)	L(0)	19.88(+)	<0.01
	Modified morphoedaphic index (conductivity adjusted for H^+)	L(10)	0.58	0.45
	Watershed to lakes area ratio	L(0)	0.04	0.84
	Littoral area (ha)	L(0)	6.49(+)	0.01
	Shoreline development index	L(0)	2.31	0.13
4	Natural reproduction and access variables			
	Lake type (0 = seepage, 1 = drainage)	0	0.83	0.36
	Number of inlets	S	4.83(+)	0.03
	Number of outlets	0	0.42	0.52
	Silica (mg/L)	L(1)	40.44(+)	<0.01
	Blocked downstream access (1 = yes, 0 = no)	0	11.90(−)	<0.01
	Spawning substrate (1 = possibly, 0 = no)	0	24.47(+)	<0.01
5	Anthropogenic control variables			
	Distance to nearest road (km)	L(1)	0.86	0.35
	Road type (1 = 2-wheel drive, 0 = 4-wheel drive)	0	0.38	0.54
	Brook trout stocked (1 = yes, 0 = no)	0	180.76(+)	<0.01
	Stocking of competitors (1 = yes, 0 = no)	0	4.59(+)	0.03
6	Biological variables			
	Presence of competitors (1 = yes, 0 = no)	0	4.72(−)	0.03
	Presence of associates (1 = yes, 0 = no)	0	79.14(+)	<0.01

[a] 0 = no transformation; L(c) = LOG10 (variable + c); S = SQRT (variable).

[b] Sign in parentheses indicates direction of effect if $P < 0.10$ (see Results section).

collinearity evaluation, variable selection, influential data identification, and model verification). Additional information particularly related to the data sets and biologically motivated decisions in the analyses, as well as additional analyses both for brook trout and for other species, can be found in Christensen et al. (1990).

Other studies have related various measures of fish status in lakes to abiotic factors. Reckhow et al. (1987) were able to develop logistic models predicting presence/absence of Adirondack brook trout and lake trout (*Salvelinus namaycush*) from water chemistry variables. Only limited success was found by Cusimano et al. (1989) in examining bivariate relationships between presence/absence of many species of fish and 19 abiotic factors in 51 lakes in the Upper Peninsula of Michigan. Other measures of fish status examined have included abundance (Cusimano et al. 1989), associations of fish species (Johnson et al. 1977), and species richness (e.g. Matuszek and Beggs 1988; Rago and Wiener 1986). As elaborated in the Discussion, most of these studies were successful in identifying strong relationships between a variety of abiotic factors and fish status in lakes, particularly when data from large numbers of lakes were available.

Methods

Prior to the analyses reported here, the data set described in the introduction was screened for correctness (e.g. appropriate magnitude and plausible value). Because stocking of brook trout is common and stocking information is not reliable for privately owned lakes, these lakes were excluded from the analyses. The data set was further reduced to include only ''qualified'' lakes: lakes not limed within 10 yr, not having suspect observations, and containing complete observations for all of the candidate variables. After these steps, the calibration data set had 444 lakes, 186 containing brook trout, and the verification data set had 216 lakes, 75 containing brook trout. A collection of variables of potential importance in explaining the distribution of fish in Adirondack lakes had already been identified and grouped into broad categories at the beginning of the ALSC study (Baker et al. 1990b). Most of the variables were potentially relevant to brook trout, and these (Table 1) were used in developing our models. The logic of including some variables in particular categories is obvious (e.g. stocking of brook trout is clearly a form of anthropogenic control), while for others it is more subtle. For example, Si is now considered a potential index of suitable habitat for brook trout natural reproduction in Adirondack lakes, probably by indicating groundwater upwelling (Schofield 1990). With respect to biological control variables, the presence of competitors could clearly have a direct negative effect on the probability of brook trout presence, while the presence in a lake of other species commonly associated with brook trout may be a surrogate for habitat suitability.

All calculations in this study were performed with the use of the Statistical Analysis System (SAS Institute, Inc. 1985a, 1985b, 1985c, 1986).

Model Development

Multiple logistic regression is a statistical procedure frequently used to build models that predict the probability of a binary response, such as the occurrence of a fish species, as a function of observable explanatory variables (in this case, quantitative information about the lakes and their watersheds) (see Hosmer and Lemeshow 1989). The logistic regression function assumes that the conditional mean, π, of the binary dependent variable, Y, for a given set of values for the explanatory variable $\boldsymbol{x} = (x_1, x_2, \ldots, x_p)'$, is given by

$$(1)\quad \pi(\boldsymbol{x}_i) = \text{Prob}\,\{\text{fish present given } \boldsymbol{x}_i\} = \exp(\beta_0 + \beta_1 x_{i1} + \ldots + \beta_p x_{ip})/(1 + \exp(\beta_0 + \beta_1 x_{i1} + \ldots + \beta_p x_{ip}))$$

where $x_{i1}, \ldots, x_{ip}$ represent the observed values of the explanatory variables for the ith observation (in this case, a given lake) and the β's are unknown parameters to be estimated by maximizing the likelihood function

$$(2)\quad l(\beta) = \prod_{i=1}^{n} \pi(\boldsymbol{x}_i)^{y_i}\,(1 - \pi(\boldsymbol{x}_i))^{1-y_i}$$

where $y_i = 1(0)$ if the fish species is present (absent) in the ith lake. The expression

$$(3)\quad g(\boldsymbol{x}) = \log[\pi(\boldsymbol{x})/(1 - \pi(\boldsymbol{x}))] = \beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p$$

is called the logit of the multiple logistic regression function. In this study, the x's correspond to the observed values or to some transformation of the explanatory variables (see Table 1) for a given lake. In order to evaluate whether differences in the values of the explanatory variables existed between the two classifications (brook trout present and brook trout absent), one of two tests was used on each explanatory variable. For the continuous variables, the nonparametric Mann–Whitney test was used to test for equality in the distributions for the two classifications. For the categorical variables (e.g. thermal stratification), a $2 \times k$ contingency table analysis (k equals number of levels of the categorical variable, usually 2) was used to test for homogeneity in the distribution of the two classifications. Although this analysis considers each variable separately and ignores the potential effect of multiple predictors, the results can be useful as a preliminary exploratory analysis to identify variables that may be useful in predicting the presence or absence of brook trout, just as simple correlations are useful in multiple linear regression.

Before using the logistic model to describe the probability of brook trout presence as a function of the collection of explanatory variables, the marginal distributions of the explanatory variables were examined separately for both values of the dependent variables (presence and absence). The purpose of this examination was to determine if these marginal distributions were highly skewed and also to determine if the variation in the two groups of lakes (lakes with brook trout present versus those with brook trout absent) was significantly different. If the distribution was found to be skewed, a form of transformation (usually log) was used so that the transformed marginal distribution did not differ significantly from a symmetric distribution. This attempt to achieve symmetric marginal distributions was also found to improve the homogeneity of variance in the two groups of lakes. The symmetry and variance homogeneity of these marginal distributions are necessary conditions for omitting interaction terms in the logistic regression function. When the explanatory variables follow a multivariate normal distribution with equal covariance matrices, the appropriate logistic function involves only linear terms of the explanatory variables (Lachenbruch 1975). Therefore, satisfying these necessary conditions would be desirable when we are using the linear logistic function as our starting approximation. Except for the variable associated with the number of inlets, where the square root transformation was used, our family of transformations was limited to the following form: $\log_{10}(x + c)$, where x is the original observed predictor variable and c is a constant. The choice of c was made to keep $x + c > 0$ and also to make use of the maximum value of x (i.e. c was restricted to be $<10\%$ of the maximum value of x). In a few cases, even when x was positive, we found that adding a nonzero value to x improved the symmetry of the marginal distribution (see Table 1).

Collinearity Diagnostics

As part of the regression analysis of a given data set, it is helpful to determine if collinearity among the explanatory variables is producing adverse effects on the resulting parameter estimates (e.g. large standard errors and counterintuitive signs of estimated coefficients). In the linear regression model, a spectral decomposition of the $X'X$ matrix, where X is the $n \times (p + 1)$ matrix of 1's in the first column and observations on the *p* explanatory variables (usually centered by subtracting the column mean and/or scaled by a constant proportional to the column standard deviation) in the remaining columns, is frequently used to evaluate the effects of collinearity on the estimated model (see Belsley et al. 1980 for a detailed discussion of this and other diagnostic tools for the multiple linear regression model). Marx and Smith (1990) suggested that a spectral decomposition of $X'VX$, the information matrix from the logistic regression model, should be used to evaluate the adverse effects of collinearity among the explanatory variables on the parameter estimation and prediction for logistic models, where V is an $n \times n$ diagonal matrix with ith diagonal element given by

$$(4) \quad \hat{\pi}(\boldsymbol{x}_i)[1 - \hat{\pi}(\boldsymbol{x}_i)]$$

where $\hat{\pi}(\boldsymbol{x}_i)$ is equal to $\pi(\boldsymbol{x}_i)$ with the maximum likelihood estimates substituted for the β's.

The eigenvalues of a scaled version of the information matrix provide a useful measure of the degree of ill-conditioning of the information matrix. Such ill-conditioning produces detrimental effects on the parameter estimates. The condition numbers, which are square roots of the ratio of the maximum eigenvalue to a given eigenvalue, are diagnostics that have already proven useful in the linear regression context. Small condition numbers indicate no adverse effects on the estimated parameters caused by collinearity. Along with the condition numbers, weighted variance inflation factors (diagonal elements of the inverse of the scaled information matrix) and variance proportions (a weighted proportion of variance associated with the jth estimated parameter that can be attributed to the ith eigenvalue of the scaled information matrix) can be used to identify the collinear variables. If the maximum condition number was greater than 30 (see Belsley et al. 1980), then the large variance proportions (e.g. >0.50) associated with the large condition number were used to identify the variables involved in the collinearity. Once these variables were identified, one of them was selected for removal from the list of candidates using a sequential list of criteria presented below. Each element in this list of criteria was applied only if consideration of all the preceeding criteria had not identified the variable to be removed.

- The intercept was always kept.
- Potentially mechanistic variables were preferred over surrogate variables for retention.
- If the collection contained some related variables and some unrelated ("isolated") variables, one of the related variables was preferred for elimination.
- At least one variable representing each of the variables pH, Al, and Ca was preferred for retention.
- Variables expected to be most important in explaining brook trout status were preferred for retention.
- Variables representing beavers, fishing pressure, bogs, or organic acidity were arbitrarily preferred for retention because these are elements of particular interest.
- Variables considered to be measured or estimated more reliably than other variables were preferred for retention.
- Variables available in the EPA's National Surface Water Survey were preferred for retention.
- Variables were preferred for retention if eliminating them would completely remove a constituent from representation. For example, the sum of base cations would be preferred for retention over the sum of Ca + Mg because, if the sum of base cations were eliminated, K would no longer be represented among the candidate variables.
- Actual observed variables were preferred for retention over composite variables. For example, lake area and mean depth would be preferred for retention over lake volume, which is derived from them.
- Continuous variables were preferred over discrete variables.
- Variables significantly associated with the response variable (i.e. those whose values differed significantly between the presence and the absence classes) were preferred for retention over those not significantly associated.
- If the criteria listed above did not identify a variable to eliminate, the variable with the larger variance proportion value or a larger variance inflation factor was used to identify a variable involved in causing the poorly estimated coefficients. This variable would then be eliminated.

This procedure was repeated until gross collinearities were resolved (i.e. until the maximum condition index was <30). Once the collinearity was resolved, the resulting subset of variables was submitted to the LOGIST procedure in SAS (SAS Institute, Inc. 1986), a logistic regression procedure with a variable selection option, for the selection of the final model. Collinearity among the explanatory variables for the final selected model was also checked by examining the final maximum condition index and the resulting parameter estimates.

Diagnostics for Influential Observations

Once the reduced model was selected by using the stepwise procedure for a logistic regression model, the logistic regression diagnostics derived by Pregibon (1981) were applied to this model with the use of a modified version of a SAS procedure by Davis (1988). Pregibon's diagnostics provide measures that indicate the influence of each observation on the following aspects of the model: (1) goodness of model estimate (i.e. How well does the model predict the sample observation?), (2) coefficient sensitivity (i.e. How much does each observation influence the parameter estimate?), and (3) goodness-of-fit sensitivity (i.e. How much does each observation influence the deviance and chi-square goodness-of-fit statistics?).

The deviance and chi-square statistics provide measures of the ability of the logistic model to predict the sample observations and are given by

$$(5) \quad D = \sum_{i=1}^{n} d_i^2$$

and

$$(6) \quad \chi^2 = \sum_{i=1}^{n} \chi_i^2,$$

respectively, where

$$(7a) \quad d_i^2 = -2\log(1 - \hat{\pi}(\boldsymbol{x}_i)), \qquad \text{if } y_i = 0,$$

$$(7b) \quad d_i^2 = -2\log(\hat{\pi}(\boldsymbol{x}_i)), \qquad \text{if } y_i = 1,$$

and

$$(7c) \quad \chi_i^2 = (y_i - \hat{\pi}(\boldsymbol{x}_i))^2/\{\hat{\pi}(\boldsymbol{x}_i)[1 - \hat{\pi}(\boldsymbol{x}_i)]\}.$$

The d_i and χ_i values may be compared with the residuals in the linear regression model that are used to identify outlying or influential data points. An examination of χ_i and d_i against i

plots will help to identify outlying or influential points. Large values of χ_i and d_i (e.g. >2 in absolute value) indicate observations poorly fit by the model. The coefficient sensitivity can be evaluated by examining the two confidence interval displacement diagnostics

(8a) $c_{1i} = \chi_i^2 h_{ii}/(1 - h_{ii})^2$

and

(8b) $\bar{c}_{1i} = \chi_i^2 h_{ii}/(1 - h_{ii})$

where h_{ii} is the ith diagonal element of the matrix

(9) $V^{1/2}X(X'VX)^{-1}X'V^{1/2}$

and X is the data matrix and the elements of V are given by equation (4). The $\bar{c}_{1i}$ statistic measures the overall change in the fitted $g(\mathbf{x})$ values as a result of deleting the ith observation for all points excluding the ith observation whereas c_{1i} includes the deleted point. Plots of c_{1i} and $\bar{c}_{1i}$ against i may be used to identify outlying or influential observations.

The diagnostics used to evaluate goodness-of-fit sensitivity are Δ deviance and Δ chi-square. The change in deviance associated with the deletion of the ith observation is given by

$$\Delta_i \text{ deviance} = d_i^2 + \bar{c}_{1i},$$

and the corresponding change in the χ^2 statistics is given by

$$\Delta_i \text{ chi-square} = \bar{c}_{1i}/h_{ii}.$$

Again, plots of these diagnostics against i can be used to identify outliers. In addition to these diagnostics, robust methods may be used to reduce the effect of unusual data on the resulting model (see Reckhow 1990).

Model Verification

As part of any model building process, it is good practice to evaluate the performance of the derived model on an independent data set (see Picard and Berk 1990). The results of this verification process can be helpful in obtaining unbiased estimates of the proportion of lakes correctly classified as having or not having brook trout. It is known that using the same data set that was used to develop the model to estimate the proportion of lakes correctly classified can give overly optimistic results (see Lachenbruch 1975).

In order to have a verification data set, the original data set was randomly divided into two parts in an approximately 2:1 ratio. The larger (calibration) subset was used to develop the models, and the smaller (verification) subset was retained for the verification process, which involves three aspects:

(1) For each lake in the verification subset, a predicted probability of presence was estimated from the derived model. If this predicted probability was greater than 0.5, we predicted that the fish species would be present in that lake. If it was less than 0.5, we predicted that the fish species would be absent from the lake. After making this estimate for all of the lakes in this data set, a classification table was constructed from which the proportion of correctly and incorrectly classified lakes could be obtained.

(2) Cohen's kappa statistic (see Titus et al. 1984) was calculated from the classification table derived from the verification data set. This statistic is used to express the proportion of lakes correctly classified by the selected model, after removing the effect of correct classification by chance, and is given by

$$\kappa = (P_0 - P_C)/(1 - P_C)$$

where P_0 is the proportion of observations correctly classified and P_C is the proportion of observations expected to be classified correctly by chance alone. P_C is calculated from the observed × predicted classification table by using the row and column proportions (i.e. P_C is the sum of row times column proportions summed over all categories). The maximum value of 1.0 indicates all observations are correctly classified. Confidence limits were also calculated for this statistic to provide us with an idea of how well the selected models are performing in predicting fish presence.

(3) The expected number of lakes with fish present is by definition equal to $\Sigma\pi(\mathbf{x}_i)$. Therefore, the sum of the predicted probabilities from the selected model is an estimate of the expected number of lakes in the verification data set with the fish species present. The predicted and observed numbers of lakes with fish present were compared.

Results

A summary from the Mann–Whitney test and contingency table analysis on the screened data set (see Methods section) is given in the last two columns of Table 1. Within each of the six variable categories, there are explanatory variables whose distributions differ significantly between the present/absent classes. The sign (+ or −) associated with each variable showing a significant ($P < 0.10$) difference indicates the "direction" of the effect of the variable on the presence or absence of brook trout. For the continuous explanatory variables, the "+" sign indicates that higher values of the variable are associated with those lakes where brook trout are present. (The "−" sign indicates lower values.) For the discrete explanatory variables, the "+" sign indicates that the odds ratio

$$\psi = \frac{P[\text{presence}|x = 1]/P[\text{absence}|x = 1]}{P[\text{presence}|x = 0]/P[\text{absence}|x = 0]}$$

is greater than 1, where $P[\text{presence}|\ x = 1]$ is the proportion of lakes with brook trout present given that the explanatory variable equals 1. Similar definitions hold for the other terms in ψ. (The "−" sign indicates a ratio less than 1.) These results help in determining the anticipated sign for the β-coefficient associated with a particular explanatory variable. However, this must be used cautiously, since the other variables are being ignored in this analysis.

The 22 explanatory variables requiring transformation to improve the symmetry and reduce the heterogeneity of variance in the presence/absence categories for the designated variables are also identified in Table 1. Notched box-and-whisker plots for seven of the transformed continuous explanatory variables are displayed in Fig. 2 in order to show the pattern of distribution for a selected subset of variables in lakes with and without brook trout for the calibration and verification data sets. For most variables, the following features were noted:

(1) There is a basic similarity in terms of location and dispersion of the distributions for the calibration subsets in comparison with the verification subsets.

(2) For most of the explanatory variables, there is a similarity of dispersion in the absence and presence categories. For both the continuous and the discrete explanatory variables, the ratio of the sample variances from the two categories was used to evaluate the homogeneity of variance of the untransformed and transformed variables. Although not shown here, this statistic

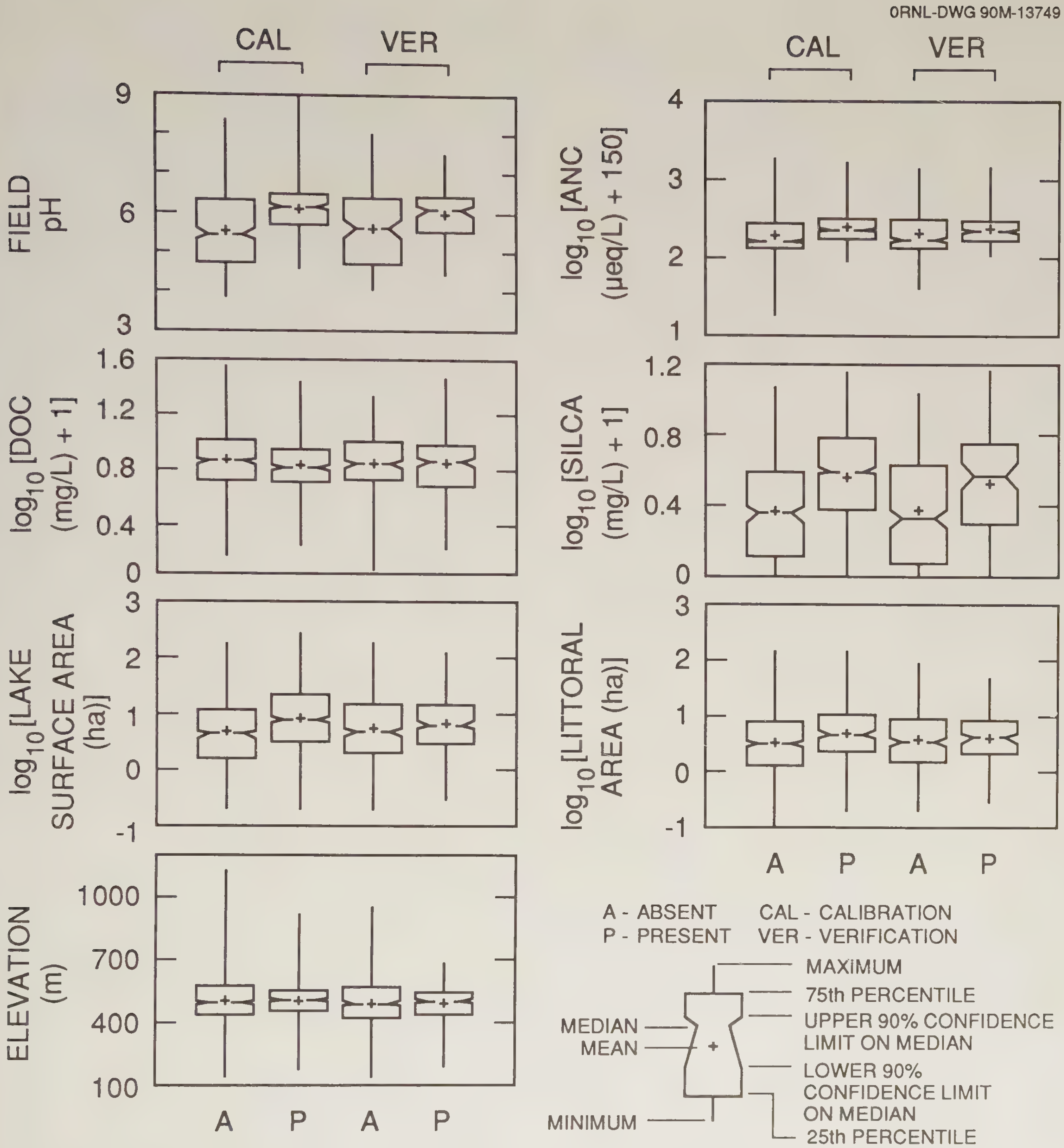


FIG. 2. Box-and-whisker plots of selected explanatory variables for calibration and verification data sets.

showed an improvement in the homogeneity of variance for the transformed variables when compared with the untransformed variables in most cases. In particular, a number of variables with extreme values for this ratio before transformation showed homogeneous variance after transformation.

(3) For most of the transformed variables, the distribution of the transformed variable was reasonably symmetric.

Symmetry and similarity of dispersion are desirable properties in the analysis, particularly for the first-order models (i.e. no interaction terms) used in our work. Pronounced differences in the values of an explanatory variable between absence and presence (e.g. as evident for field pH and Si) would lead one to expect that explanatory variable to be an important predictor in the final models. However, it is important to remember that these are univariate relationships whereas the models consider joint or multivariable relationships. Results are, therefore, far from completely predictable from the univariate patterns.

Once the collection of candidate explanatory variables was identified and transformed as needed, the next step was to determine if collinearity is having an adverse effect on the initial model. The results from the collinearity diagnostics along with the variables omitted are summarized in Table 2. The most

TABLE 2. Candidate variables involved in multicollinearities and variables eliminated from the candidate list (indicated by an asterisk) at each step of the initial collinearity analysis for brook trout. Large values (>30) of the maximum condition number imply numerical problems with the estimated parameters.

Step	Number of variables	Maximum condition number	Variables involved in multicollinearity
1	41	280.1	Volume*, area, mean depth
2	40	69.58	Ca + Mg*, sum of base cations
3	39	65.49	Full bog*, intercept
4	38	48.25	Modified morphoedaphic index*, area, mean depth, littoral area
5	37	43.67	pCa/pH*, field pH, Ca
6	36	40.08	Na*, Ca, sum of base cations
7	35	29.95	Area, littoral area

adverse collinearity was among the volume, area, and depth variables (condition number of 280), a not-unexpected result, since the volume is a function of lake depth and area. With the elimination of only six variables, the maximum condition number was reduced to a value <30. If we use the same limits on the maximum condition index as suggested with the linear regression model (Belsley et al. 1980), this value would imply that moderate-to-strong collinearities have been eliminated.

Two sets of candidate variables were used in the stepwise selection. Variable set V1 is the full set of relevant noncollinear explanatory variables. It is based on the full set of 41 variables in Table 1, minus the six variables shown in Table 2 eliminated due to collinearity. It includes the two biological variables presence of associates and presence of competitors, which have clear potential for explaining brook trout presence or absence, respectively. However, because lakes where brook trout status was unknown would lack the biological sampling needed to evaluate the presence of associates and presence of competitors, these variables would not be available for predicting brook trout status in such lakes. Both because of interest in making predictions for lakes with unknown brook trout status and because we wanted to see what variables would be selected if these biological variables were not available as part of the "explanation" of brook trout status, we also developed a model starting with set V1, but with these two variables removed. This set of 33 variables, lacking the two biological variables, is designated variable set V0.

Results from the stepwise logistic regression analysis using variable sets V1 and V0 are shown in Tables 3 and 4, respectively. Variables selected as significant are listed with their coefficients as estimated from standardized data (where the explanatory variables have been shifted and scaled by their means and standard deviations, respectively) as well as their significance level and nonscaled coefficients based on the nonstandardized data. The sign of the coefficient indicates whether the variable's effect on the occurrence of brook trout is predicted to be positive or negative (given the effects of the other variables in the model). The relative importance of the variables is indicated in two ways. If the explanatory variables are uncorrelated, the absolute magnitudes of the standardized coefficients within a given model provide a measure of the relative importance of the variables. In addition, smaller values of the entries in the significance column also tend to indicate more important variables. Although these two measures of importance do not always agree, they tend to follow similar patterns. Calibration and verification tests of the models are presented in Table 5.

For variable set V0, without the competitors and associates variables, the logistic regression diagnostics of Pregibon (1981) were calculated to identify influential observations by using the selected model given in Table 4. After an examination of these diagnostics, three lakes were found to have outlying (large) values, relative to the remaining data, for at least four of the diagnostic measures presented in the Methods section. The three observations were omitted and the reduced data resubmitted to obtain new diagnostic measures. At this second pass, 18 additional lakes were identified as being potentially influential, i.e. large values for some of the diagnostic measures. A summary of the diagnostic measures for the 21(=3 + 18) lakes identified is given in Table 6. Because variable set V0 is of broader general applicability, we only identified influential observations for this variable set.

As a final comparison, the eight-variable model was fit to the following data sets: (1) full data set of 444 observations, (2) phase one data set of 441 (=441 − 3) observations, and (3) phase two data set of 423 (=444 − 21) observations.

The results of this process are summarized in Table 7. The estimates for all of the parameters increase in absolute magnitude, indicating a more sharply focused model (i.e. the change in the estimated probability of a fish species being present is

TABLE 3. Variables (biological variables included), listed in order of the absolute magnitude of their shifted and scaled coefficients, selected to explain the presence of brook trout in qualified nonprivate calibration lakes. Stepwise selection, starting with variable set V1 (35 noncollinear brook trout candidate variables), was used to identify these variables.

Variable[a]	Nonscaled coefficient	Significance	Standardized coefficient	Variable group[b]
Stocking of brook trout	5.40034	<0.0001	49.9914	5
Presence of associates	3.58819	<0.0001	36.8326	6
pH	1.25419	0.0019	21.5926	1
Presence of competitors	−2.29225	<0.0001	−20.4563	6
Silica (T)	3.15346	<0.0001	19.1955	4
Acid-neutralizing capacity (T)	−3.46063	0.0201	−14.4337	1
Distance to nearest road (T)	1.64951	0.0038	12.3106	5
Dissolved organic carbon (T)	−2.74330	0.0071	−11.4237	1
Substrate	1.06374	0.0156	9.8472	4
Intercept	−3.21075	0.2274		

[a] The notation (T) after a variable denotes that a transformed form of the variable was used.

[b] Variable groups are defined in Table 1.

TABLE 4. Variables (biological variables excluded), listed in order of the absolute magnitude of their shifted and scaled coefficients, selected to explain the presence of brook trout in qualified nonprivate calibration lakes. Stepwise selection, starting with variables set V0 (33 noncollinear brook trout candidate variables, excluding biological variables), was used to identify these variables.

Variable[a]	Nonscaled coefficient	Significance	Standardized coefficient	Variable group[b]
Stocking of brook trout	4.83308	<0.0001	44.7402	5
pH	1.51466	<0.0001	26.0770	1
Silica (T)	3.22266	<0.0001	19.6112	4
Acid-neutralizing capacity (T)	−2.63705	0.0361	−10.9987	1
Distance to nearest road (T)	1.43208	0.0038	10.6879	5
Substrate	0.97254	0.0091	9.0029	4
Blocked downstream access	−0.53996	0.0738	−5.6722	4
Road type	−0.64659	0.0607	−5.5659	5
Intercept	−6.15828	0.0043		

[a] The notation (T) after a variable denotes that a transformed form of the variable was used.
[b] Variable groups are defined in Table 1.

TABLE 5. Summary of calibration and verification results for brook trout models.

(a) Calibration statistics

Variable set[a]	Concordance C	Kappa (asymptotic 95% conf. int.)	Classification table (prior = 0.5) Observed	Predicted Absences	 Presences	 Total
V1	0.954	0.76	Absences	240	18	258
		(0.70, 0.82)	Presences	33	153	186
			Total	273	171	444
V0	0.921	0.72	Absences	242	16	258
		(0.65, 0.79)	Presences	43	143	186
			Total	285	159	444

(b) Verification statistics

Variable set[a]	Number of lakes containing brook trout Observed	Predicted $\Sigma\ \hat{\pi}(x_i)$	 Classification table	Kappa (asymptotic 95% conf. int.)	Classification table (prior = 0.5) Observed	Predicted Absences	 Presences	 Total
V1	75	86.6	78	0.63	Absences	121	20	141
				(0.51, 0.74)	Presences	17	58	75
					Total	128	78	216
V0	75	84.7	69	0.56	Absences	123	18	141
				(0.44, 0.68)	Presences	24	51	75
					Total	147	69	216

[a] *Variable set V1 includes the biological variables (presence of associates, presence of competitors). Variable set V0 does not include these biological variables.*

more abrupt for a given change in an explanatory variable). This implies that the resulting model should do a better job of estimating the presence of fish in a given lake, and the concordance values for these models reflect this. In order to determine the concordance statistic, one considers all pairs of observations with different Y values and counts the number of pairs for which the observation with the larger Y has a higher predicted probability than does the observation with the smaller Y. The concordance statistic equals the fraction of concordant pairs plus one half the fraction of tied pairs. The order-of-magnitude increase in the coefficient associated with brook trout stocking, along with the increase in its associated standard error, is caused by the fact that in the last pass ($N = 423$), all of the lakes that had been stocked with brook trout but had no brook trout present were eliminated because of their influence on the results. Therefore, numerical problems arise.

Discussion

As evidenced in Table 5a, both of the models do a good job of predicting the presence of brook trout from the selected models for the calibration data set. In particular, the kappa sta-

TABLE 6. Summary of influential lakes from Pregibon (1981) diagnostics for variable set V0.

Lake number	Stage identified[a]	Diagnostic summary[b] *a*	*b*	*c*	*d*	*e*	*f*
020008	2			×	×	×	
020059	2					×	×
020128	2	×	×	×	×	×	×
020384	2	×				×	×
020393	2			×	×	×	
030182	2	×	×	×	×	×	×
030266	2	×	×	×	×	×	×
030268	2			×	×	×	×
030273	1	×	×			×	×
040316	1	×	×	×	×	×	×
040352	2	×	×	×	×	×	×
040379	2	×	×	×	×	×	×
040753	2	×	×	×	×	×	×
040852	2	×	×	×	×	×	×
040887	2	×	×			×	×
040995	2			×	×	×	
041007	2	×	×	×	×	×	×
050368	1	×	×	×	×	×	×
050465a	2	×	×	×	×	×	×
050671	2	×	×			×	×
070770	2	×				×	×

[a] *1 = first pass; 2 = second pass with reduced data set (n = 444 − 3 = 441 observations).*

[b] *Entry of "×" indicates significant diagnostic. Poorly fit observations: a = abs (deviance component) > 2; b = abs(chi-square component) >3. Coefficient sensitivity: $c = c_1 > 0.2$; $d = \bar{c}_1 > 0.2$.* Goodness-of-fit sensitivity: $e = \Delta$ deviance > 2.0; $f = \Delta$ chi-square > 6.0.

tistics were large (>0.70) for both models, and the proportion of correctly classified lakes was 0.89 for V1 and 0.87 for V0. A better idea of the selected model's ability to predict the presence of brook trout can be obtained from the results in Table 5b than from those in Table 5a. Because the same data are being used to select the model as well as to evaluate its predictive ability, the results in Table 5a probably are overly optimistic. However, the results in Table 5b still are encouraging (e.g. proportions >0.80 of correctly classified lakes for both variable sets, kappa statistics >0.50, and number of lakes predicted to contain brook trout within 15% of the actual number for both variable sets).

There were six explanatory variables that were selected for both of the variable sets (see Tables 3 and 4). In both models, the magnitude and sign of the coefficients associated with these explanatory variables are similar. Because the evaluation of the importance of acidification response variables (Group 1) was a primary goal of this study, it is interesting to note that the variable pH was highly significant in both models, and its sign was as expected. However, another acidification response variable, acid-neutralizing capacity (ANC), is significant in both models, but with a negative sign. This finding is unexpected because ANC has a significant positive association with brook trout presence (Table 1). It is well known that ANC is significantly, positively, and nonlinearly related to pH (Munson et al. 1990). A possible explanation for the effect of ANC in the model is that, at a fixed pH, a higher value of ANC may indicate the presence of greater organic acidity.

The occurrence of pairs of similar variables (such as the pH–ANC pairing) and sign switching can be interpreted as a warning against overinterpreting the importance and effect of individual variables selected in these models. For example, with 30 candidate variables, there are 2^{30} (i.e. more than a billion) combinations of variables and, therefore, the same number of possible models. Although because of the collinearity analysis the variables retained as candidates are not grossly collinear, some of the variables may nonetheless be related to each other and to a large degree may be able to substitute for each other.

The application of the logistic regression diagnostics was helpful in identifying those observations that have a large influence on the estimated model. In the second phase of this exercise, we noted that all the lakes with no brook trout present that had been stocked with brook trout were eliminated. This means that we should consider eliminating this stocking variable in subsequent analyses of this reduced data set because we cannot estimate its effect precisely. However, it would also be reasonable to remove the stocked lakes from the analyses, and perhaps to arbitrarily classify them as having brook trout present. After a collection of lakes has been identified as being "influential" on the derived model, as a next step, the infor-

TABLE 7. Summary of parameter estimates with and without influential observations for brook trout eight-variable model using variable set V0.

Parameter	Estimates (standard error) 444 observations	441 observations	423 observations
Stocking of brook trout	4.8331 (0.5394)	5.6179 (0.6627)	15.1779 (21.7828)
pH	1.5147 (0.3532)	1.7256 (0.3783)	2.9159 (0.5690)
Silica (T)	3.2227 (0.6349)	3.6955 (0.6823)	6.2215 (1.0485)
Acid-neutralizing capacity (T)	−2.6370 (1.2579)	−3.2300 (1.3182)	−5.3750 (1.7293)
Distance to nearest road (T)	1.4321 (0.4943)	1.5314 (0.5220)	2.6578 (0.7164)
Substrate	0.9725 (0.3731)	1.0571 (0.3931)	1.7617 (0.5549)
Blocked downstream access	−0.5400 (0.3020)	−0.6058 (0.3182)	−0.9377 (0.4236)
Road type	−0.6466 (0.3447)	−0.7987 (0.3614)	−1.5206 (0.4842)
Intercept	−6.1583 (2.1578)	−6.2763 (2.2656)	−10.6827 (3.1712)
Goodness-of-fit statistics			
Chi-square	570.2 ($P < 0.001$)	359.5 ($P > 0.50$)	172.8 ($P > 0.50$)
Deviance	301.4 ($P > 0.50$)	274.9 ($P > 0.50$)	167.0 ($P > 0.50$)
Degrees of freedom	435	432	414
Concordance	0.921	0.931	0.974

mation on these lakes could be closely examined to determine if (1) potential errors exist in the recorded data for the data at the identified lake, (2) different measurement techniques were used in obtaining the information for the suspect lake, or (3) the values for the explanatory and response variables are implausible. In addition, the geographic location of the ''influential'' lakes, relative to the remaining ones in the data set, could be examined to see if these lakes are clustered together in a relatively small subarea of the total sampled area. The results of this investigation could be helpful in deciding if modifications need to be made in the proposed model (e.g. the inclusion of some additional interaction-type terms).

In summary, Groups 4 (natural reproduction and access variables) and 6 (biological variables, when available to the model) are consistently important. Brook trout are less likely to be caught in lakes supporting one or more species considered as potential competitors (e.g. yellow perch (*Perca flavescens*) or largemouth bass (*Micropterus salmoides*)) and more likely to be caught in lakes where fish species commonly associated with brook trout were caught. Brook trout are also more likely to be caught in lakes with high levels of Si, which appear to indicate greater groundwater input and, therefore, a greater likelihood of suitable spawning habitat (Schofield 1990). Group 1 (acidification response variables) is represented by pH and is highly important. Group 5 (anthropogenic variables) is very important when stocking is available to the model and is represented by distance to the nearest road when stocking information is not available. Groups 2 (baseline habitat suitability variables) and 3 (productivity-related variables) were not represented in either of these models. Additional models constructed for other groups of lakes (particularly for groups of lakes where stocking cannot be used as a predictor variable) did contain variables from these groups (Christensen et al. 1990). Nonetheless, these variables from Groups 2 and 3 never achieved as high a level of importance in the models as did the highly significant variables discussed previously. When models were constructed for lakes known not to have been stocked, there were both similarities and differences between those models and the models discussed previously. The models were most similar when, in addition to the stocking variable, the biological variables (presence of competitors or presence of associates) were also not included in the model building process.

Other studies have been conducted of fish presence/absence, abundance, species associations, and species richness as functions of abiotic factors in lakes. Reckhow et al. (1987), using data from Adirondack lakes which historically contained the target species, examined the relationships between the presence/absence of four fish species and four acidification-related predictor variables (pH, Al, Ca, and alkalinity). Numbers of lakes available for particular models varied widely depending on the combination of species and predictor variables, ranging from 0 for yellow perch and Al to 210 for lake trout and alkalinity. Successful logistic regression models were developed for brook trout and lake trout. Reliable models could not be developed for white sucker (*Catostomus commersoni*) or yellow perch, although such a model for white sucker might have been possible if Al data had been available for more lakes. Cusimano et al. (1989) examined a series of bivariate relationships between 19 abiotic factors and the presence/absence of three grouped and 21 individual fish species, including brook trout, in 51 lakes in the Upper Peninsula of Michigan. Eight variables were identified as significant in explaining the presence of four individual fish species, not including brook trout (which were present in only four of the 49 lakes). Perhaps due to highly variable catch efficiency, little success was found in relating these factors to abundance of the eight fish species (not including brook trout) for which data were considered adequate.

Johnson et al. (1977) defined 15 lake types, representing associations of four gamefish species, and related these to abiotic characteristics of 2496 Ontario lakes using a canonical discriminant analysis. Fishless lakes were not included. The importance of various factors in each canonical equation differed depending on its role in separating either single species, particular groups of species, or the complexity of associations. Mean depth, Secchi depth, lake size (shoreline development and area), and pH were identified as the main factors in one or more of the first three primary canonical equations.

Fish species richness has been studied frequently in relation to abiotic variables. Using a subset of the ALSC data, pairwise associations between species richness (the number of species caught) and a number of predictor variables were used to identify key variables of interest, as well as a set of candidate models involving these variables (Baker et al. 1990a). Models were then developed and tested on two additional subsets of the data. The best overall model of species richness included pH, surface area, elevation, Si, Ca, and a pH × Ca interaction term. Using 992 Ontario lakes for which data on 19 physical and chemical variables were available, Matuszek and Beggs (1988) used stepwise multiple regression analysis to identify lake area, total Al, latitude, dissolved organic carbon (DOC), and elevation as the most significant variables in explaining species richness; lake area was the most important. When lakes with $\mathrm{pH} < 6$ were examined, pH, elevation, lake area, and DOC were identified as most important. Because acidic lakes tend to be smaller, the effect of area can confound interpretation of the effect of pH on species richness in field data. Rago and Wiener (1986) developed a method for removing the effects of lake area when comparing fish species richness in low-pH and high-pH lakes. With this method, low-pH lakes in six data sets from Ontario and northern Wisconsin contained significantly fewer fish species than lakes with high pH when the effect of lake area was considered.

Some of the variables identified as significant in the two models in Tables 3 and 4 were also found to be significant in these other studies, particularly pH, Si, and DOC. Most of the other significant explanatory variables in our models were not available in these studies: stocking of brook trout, presence of other associated species or of competing species, distance to and type of the nearest road, substrate type, and blocked downstream access (dams). Overlap of some selected variables would be expected. For example, pH will always be stressful at sufficiently low levels. Depending on the distribution of pH values in relation to the sensitivity of the fish species, it would always have the potential to be significant. Extensive overlap in the variables selected would, however, not necessarily be expected for a number of other reasons. Our dependent variable, presence/absence of brook trout, is qualitatively different from dependent variables such as species richness or associations of species. Many explanatory variables, such as Si (perhaps representing groundwater upwelling, indicating suitable brook trout spawning habitat), would be significant only for selected species for which they had relevance.

The models described here and other related models developed with these protocols were helpful in understanding the distribution of fish species in the Adirondacks (Baker et al. 1990b). Similar models were developed using data from relatively high-pH lakes, both inside the Adirondacks and elsewhere (Baker et al. 1990a). Acidity in these lakes was not expected to affect the probability of fish presence. These models were used to predict the baseline probability of presence of brook trout (i.e. with respect to factors other than acidity) in lakes. In combination with acidification response models (Baker et al. 1990a), these models were used to assess the consequences of different emission strategies for the control of acidic deposition (NAPAP 1991).

Acknowledgments

The authors wish to thank Jan M. Coe and Jean A. Shaakir-Ali for extensive work in adapting parts of the Adirondack Lakes Survey Corporation (ALSC) data bases for our purposes and James Gallagher for assisting us, especially with checking the results. Dr. Joan P. Baker played a key role in the process of defining appropriate variables and made many helpful suggestions during her analyses and in her review of this manuscript. We also thank Darryl J. Downing, Yetta Jager, and the journal referees for helpful comments that led to improvements in this paper. This research was sponsored in part by ALSC under contract ERD-88-778 with the U.S. Department of Energy (DOE) and in part by the U.S. Environmental Protection Agency (EPA) as a part of the National Acid Precipitation Assessment Program under Interagency Agreement DOE No. 1824-1808-Al (EPA No. DW89932112-01) with the U.S. Department of Energy, under contract No. DE-AC05-84QR21400 with Martin Marietta Energy Systems, Inc. This is publication No. 3841, Environmental Sciences Division, Oak Ridge National Laboratory. Although a part of the research described in this manuscript has been funded by EPA, it has not been subjected to EPA review and therefore does not necessarily reflect the views of EPA; therefore, no official endorsement should be inferred.

References

Baker, J. P., D. P. Bernard, S. W. Christensen, M. J. Sale, J. Freda, K. Heltcher, D. Marmorek, L. Rowe, P. Scanlon, G. Suter, W. Warren-Hicks, and P. Welbourn. 1990a. Biological effects of changes in surface water acid–base chemistry. NAPAP Report 13. *In* National Acid Precipitation Assessment Program, Acidic Deposition: State of Science and Technology. Vol. II. NAPAP, Washington, DC.

Baker, J. P., S. A. Gherini, S. W. Christensen, C. T. Driscoll, J. Gallagher, R. K. Munson, R. M. Newton, K. H. Reckhow, and C. L. Schofield. 1990b. Adirondack Lakes Survey: an interpretive analysis of fish communities and water chemistry, 1984–1987. Adirondack Lakes Survey Corporation, Ray Brook, NY.

Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. Regression diagnostics: identifying influential data and sources of collinearity. John Wiley & Sons, New York, NY.

Christensen, S. W., J. J. Beauchamp, J. A. Shaakir-Ali, J. M. Coe, J. P. Baker, E. P. Smith, and J. Gallagher. 1990. Patterns of fish distribution in relation to lake/watershed characteristics: regression analysis and diagnostics. Appendix A. *In* Adirondack Lakes Survey: an interpretive analysis of fish communities and water chemistry, 1984–1987. Adirondack Lakes Survey Corporation, Ray Brook, NY.

Cusimano, R. F., J. P. Baker, W. J. Warren-Hicks, V. Lesser, W. W. Taylor, M. C. Fabrizio, D. B. Hayes, and B. P. Baldigo. 1989. Fish communities in lakes in Subregion 2B (Upper Peninsula of Michigan) in relation to lake acidity. EPA/600/3-89/021, U.S. Environmental Protection Agency, Washington, DC.

Davis, C. S. 1988. Detection of influential observations in logistic regression using the SAS system, p. 964–969. *In* Proceedings of the 13th Annual SAS Users Group International Conference. SAS Institute, Cary, NC.

Hosmer, D. W. Jr., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, New York, NY.

Johnson, M. G., H. H. Leach, C. K. Minns, and C. H. Olver. 1977. Lomnological characteristics of Ontario lakes in relation to associations of walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and smallmouth bass (*Micropterus dolomieui*). J. Fish. Res. Board Can. 34: 1592–1601.

Kretser, W., J. Gallagher, and J. Nicolette. 1989. Adirondack Lakes Study, 1984–1987: an evaluation of fish communities and water chemistry. Prepared for Adirondack Lakes Survey Corporation, Ray Brook, NY.

Lachenbruch, P. A. 1975. Discriminant analysis. Hafner Press, New York, NY.

Marx, B. D., and E. P. Smith. 1990. Weighted multicollinearity in logistic regression: diagnostic and biased estimation techniques with an example from lake acidification. Can. J. Fish. Aquat. Sci. 47: 1128–1135.

Matuszek, J. E., and G. L. Beggs. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1931–1941.

Munson, R. K., C. T. Driscoll, and S. A. Gherini. 1990. Phenomenological analysis of fish communities in Adirondack lakes. Section 2.3. *In* Adirondack Lakes Survey: an interpretive analysis of fish communities and water chemistry, 1984–1987. Adirondack Lakes Survey Corporation, Ray Brook, NY.

National Acid Precipitation Assessment Program (NAPAP). 1991. 1990 Integrated assessment. National Acid Precipitation Assessment Program, 722 Jackson Place, NW, Washington, DC. March 1991.

Picard, R. R., and K. N. Berk. 1990. Data splitting. Am. Stat. 44: 140–147.

Pregibon, D. 1981. Logistic regression analysis. Ann. Stat. 9(4): 705–724.

Rago, P. J., and J. G. Wiener. 1986. Does pH affect fish species richness when lake area is considered? Trans. Am. Fish. Soc. 115: 438–447.

Reckhow, K. H. 1990. Robust estimation. Appendix B. *In* Adirondack Lakes Survey: an interpretive analysis of fish communities and water chemistry, 1984–1987. Adirondack Lakes Survey Corporation, Ray Brook, NY.

Reckhow, K. H., R. W. Black, T. B. Stockton, Jr. J. D. Vogt, and J. G. Wood. 1987. Empirical models of fish response to lake acidification. Can. J. Fish. Aquat. Sci. 44: 1432–1442.

SAS Institute, Inc. 1985a. SAS user's guide: basics, version 5 edition. Cary, NC.

1985b. SAS user's guide: statistics, version 5 edition. Cary, NC.

1985c. SAS/IML user's guide, version 5 edition. Cary, NC.

1986. SAS supplemental library user's guide, version 5 edition. Cary, NC.

Schofield, C. 1990. Habitat suitability for brook trout natural reproduction in Adirondack Lakes. Section 3.3. *In* Adirondack Lakes Survey: an interpretive analysis of fish communities and water chemistry, 1984–1987. Adirondack Lakes Survey Corporation, Ray Brook, NY.

Titus, K., J. A. Mosher, and B. K. Williams. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. Am. Midl. Nat. 111: 1–7.

Population Dynamics, Numerical Production, and Potential Predation Impact on a Meiobenthic Copepod[1]

James T. Morris and Bruce C. Coull

Department of Biological Sciences and Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, SC 29208, USA

Morris, J. T., and B. C. Coull. 1992. Population dynamics, numerical production, and potential predation impact on a meiobenthic copepod. Can. J. Fish. Aquat. Sci. 49: 609–616.

From the fecundity and temperature-dependent development times of the life stages of *Microarthridion littorale* and long-term measurements of the densities of copepodites and female and male adults in subtidal sediments at North Inlet, South Carolina, we calculated maximum and minimum productivity limits of this meiobenthic copepod. The potential production of numbers of nauplii (10 002 × $10^3 \cdot m^{-2} \cdot yr^{-1}$) exceeds the population density and production of copepodites and adults by about 2 orders of magnitude; observed populations of copepodites and adults can be supported even with a 98% mortality of nauplii. This suggests that predation or other causes of nauplii mortality limits the population density of *M. littorale* at North Inlet. The potential dry biomass production of nauplii is about 2.0 $g \cdot m^{-2} \cdot yr^{-1}$ and greatly exceeds the combined biomass production of copepodites and adults. Because the minimum numerical productivity (that required to explain the temporal changes in population size) of adults (38 × $10^3 \cdot m^{-2} \cdot yr^{-1}$) is 26% of the maximum potential adult productivity (derived from the maturation of copepodites), it is likely that adult densities are regulated by recruitment. A time series of population data indicates large interannual variations in production of the different developmental stages, with potential naupliar recruitment showing the greatest variability.

Les auteurs ont calculé les limites minimale et maximale de la productivité du copépode méiobenthique *Microarthridion littorale* à partir de son taux de fécondité et du temps de développement lié à la température des divers stades, ainsi que de mesures à long terme de la densité du stade copépodite et des adultes mâles et femelles dans les sédiments infralittoraux de l'inlet North, en Caroline du Sud. La production potentielle de nauplies (10 002 × $10^3 \cdot m^{-2} \cdot an^{-1}$) est supérieure à la densité de la population et à la production du stade copépodite et d'adultes par environ deux ordres de grandeur; les populations observées du stade copépodite et d'adultes peuvent être renouvelées même lorsque le taux de mortalité des nauplies atteint 98 %. Ceci porte à croire que la prédation ou d'autres facteurs de mortalité des nauplies limitent la densité de la population de *M. littorale* dans l'inlet North. La production potentielle de nauplies exprimée en biomasse sèche s'élève à environ 2,0 $g \cdot m^{-2} \cdot an^{-1}$; elle est aussi nettement supérieure à la production combinée, en biomasse, du stade copépodite et d'adultes. Étant donné que la productivité numérique minimale (soit celle requise pour expliquer les variations temporelles de la taille de la population) des adultes (38 × $10^3 \cdot m^{-2} \cdot an^{-1}$) s'élève à 26 % de la productivité potentielle maximale d'adultes (dérivée de la maturation du stade copépodite), il est probable que le recrutement régit la densité des adultes. Une série temporelle de données sur la population révèle l'existence d'importantes variations interannuelles de la production des divers stades de développement, en particulier du recrutement potentiel de nauplies.

Received March 19, 1991
Accepted October 4, 1991
(JA958)

Reçu le 19 mars 1991
Accepté le 4 octobre 1991

The copepod *Microarthridion littorale* (Poppe) is a common meiobenthic component of estuarine muds worldwide, and in subtidal muddy sediments of North Inlet, South Carolina, it is numerically the codominant copepod (Coull and Vernberg 1975; Coull and Dudley 1985). In 17 yr (1973–89) of replicate monthly (1973–80) or fortnightly (1981–89) samples, *M. littorale* comprises 18% of the total mud-dwelling copepod fauna (Coull and Dudley 1985; B. C. Coull, unpubl. data). In subtidal South Carolina muds, *M. littorale* is a continuous breeder (sensu Hicks 1979), i.e. ovigerous females are present in the population year-round (Coull and Vernberg 1975).

Because *M. littorale* is so common in North Inlet, and relatively easy to culture, a great deal of information is available on the population and life history characteristics of the species. We know the seasonal patterns of abundance in the subtidal (Coull and Dudley 1985) and intertidal zones (Fleeger 1979; Palmer 1980), the distribution of the species across tidal/elevation gradients (Coull et al. 1979; Palmer and Brandt 1981; Coull and Feller 1988), its reproductive periodicities in the subtidal (Coull and Vernberg 1975; Coull and Dudley 1985) and intertidal zones (Fleeger 1979; Palmer 1980), its development time in the laboratory at different temperatures (Coull and Dudley 1976; Palmer and Coull 1980), its abundance in fish guts (Feller et al. 1990), the number of eggs per female (Coull and Dudley 1976), and an estimate of its in situ production over a short time span (Fleeger and Palmer 1982). Despite all this information, accurate estimates of the actual annual production have been elusive because of the difficulty in measuring turnover rates of the different life stages in the field. However, it is possible to place maximum and minimum limits on production by simulating the life history characteristics of *Microarthridion*.

---

[1] Contribution No. 891 from the Belle W. Baruch Institute.

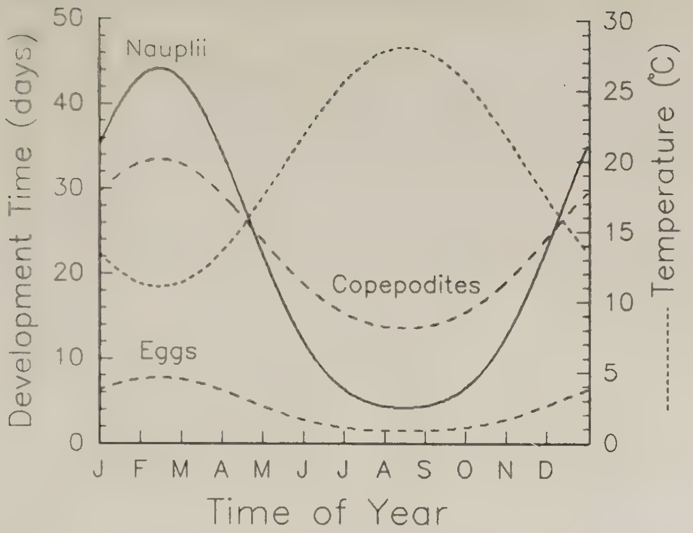


FIG. 1. Development times for eggs maturing into nauplii, nauplii maturing into copepodites, and copepodites maturing into adults as computed by Eq. 1–4 incorporating temperature responses derived by Palmer and Coull (1980) and mean daily water temperature from Clam Bank station, North Inlet, South Carolina.

The primary goal of this study was to determine what levels of mortality and recruitment are required to maintain the population sizes of copepodites and adults at levels recorded in the long-term data set, given the known fecundities and temperature-dependent development times of the different life stages. It was also possible to determine the life stage at which maximum mortality occurs and to provide estimates of the dependence of productivity on temperature. Finally, it was possible to provide insight into the regulation of population dynamics, whether by bottom-up control from the recruitment of individuals into the population or by top-down controls from predation or other sources of mortality on the adults.

Model Formulation and Results

Development Time

Development times of each life stage are temperature dependent. These are known from laboratory studies and can be estimated by the following polynomial equations (Palmer and Coull 1980):

(1) $E = 16.34 - 0.95 \times T + 0.015 \times T^2$

(2) $N = 100.8 - 6.25 \times T + 0.1 \times T^2$

(3) $C = 5.55 - 2.34 \times T + 0.03 \times T^2$

where E, N, and C refer the development times (days) of eggs, nauplii, and copepodites, respectively, and T is temperature (degrees Celsius).

Daily mean temperature (Fig. 1) was derived by fitting a trigonometric function to local water temperatures measured daily between 1988 and 1990 inclusive (Clam Bank station, North Inlet, SC):

(4) $T = T_m + T_a \sin(t2\pi/365 - \tau)$

where T is the daily mean water temperature (degrees Celsius), T_m is the mean annual temperature (19.5°C), T_a is the seasonal amplitude (8.5°C), t is the day of the year, and τ is a phase shift parameter (2.34 radians) that positions the times of maximum and minimum temperature. Computed development times throughout the year for eggs, nauplii, and copepodites are given in Fig. 1.

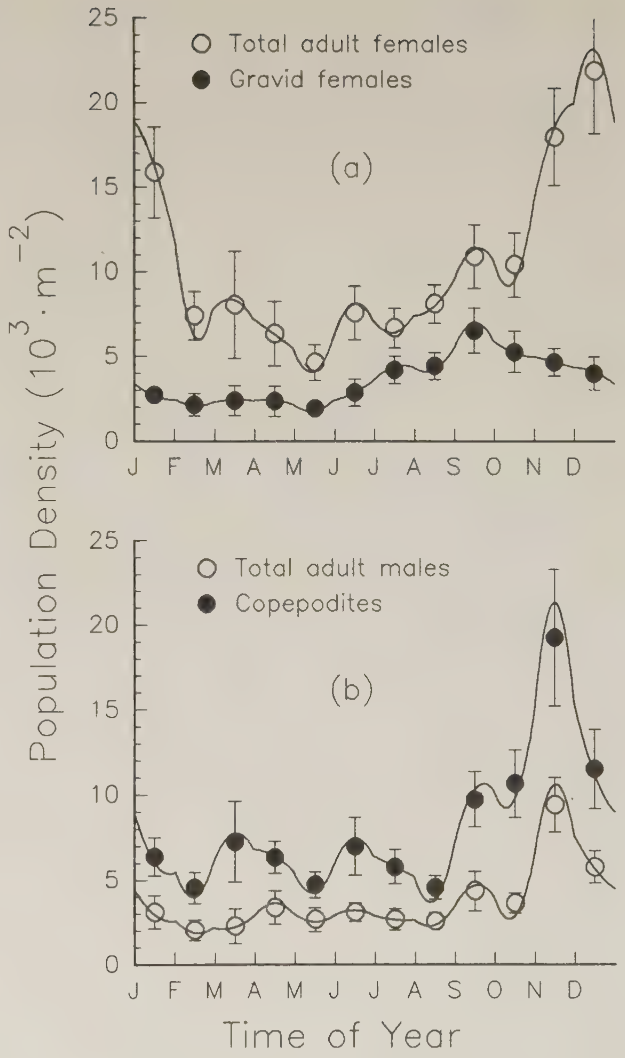


FIG. 2. Observed mean (±1SE) monthly population densities taken from 17 yr of monthly or biweekly collections for (a) total adult and gravid females and (b) copepodites and adult males. The smooth distributions (—) were generated by piecewise fitting of a second-degree polynomial to the observed data.

Population Density

In every sample from the 17-yr data set, all adult *M. littorale* were identified to sex and all copepodites were enumerated; nauplii were not counted. Unless there is a monospecific population or culture, benthic copepod nauplii cannot be separated to species without tediously mounting each specimen; even then, species-specific naupliar characteristics are often so slight that in practice, benthic nauplii are not typically distinguished to species in field samples.

Using the sex and copepodite data from the long-term data set, we fitted a second-degree polynomial function to estimates of mean abundance by month of copepodite and adult populations (Fig. 2) in order to generate time-dependent distributions of population density. The polynomial was fitted piecewise to the monthly population data. First we specified the end points of the curve which correspond to the population size at the beginning and end of each month. We took the average of adjacent monthly mean population sizes to compute these end points. For example, the adult female population size at the first and last of a month was calculated as

(5) $P_f(0) = [P_M(j-1) + P_M(j)]/2$

and

(6) $P_f(L) = [P_M(j+1) + P_M(j)]/2$

where $P_f(0)$ and $P_f(L)$ are the population sizes of females at the beginning and end of month j and the P_M are the observed monthly mean population sizes. Following this, we equated the monthly mean (P_M) to the definite integral of the polynomial:

$$(7)\quad P_M(j) = 1/L\int_0^L a_1 + a_2D + a_3D^2dD$$
$$= a_1 + a_2L/2 + a_3L^2/3$$

where L is the number of days in month j, D is the day of the month, and the a_i are coefficients that have unique solutions which are determined by Eq. 5, 6, and 7. The coefficient a_1 is equal to the population size at the beginning of the month ($D = 0$):

(8) $a_1 = P_f(0)$

and the population size on the last day of the month (L) is

(9) $P_f(L) = a_1 + a_2L + a_3L^2$.

Now there are three equations (7, 8, and 9) with three unknowns (a_i). After substituting and rearranging, the value of a_3 is calculated as

(10) $a_3 = (3/L^2)[P_f(0) + P_f(L)] - (6/L^2)P_M(j)$.

Finally, the last coefficient (a_2) was computed after substituting the numerical values of a_3 (from Eq. 10) and a_1 (from Eq. 8) into Eq. 9. This procedure was repeated for every month of data and for each set of population data and resulted in the continuous distributions of adult females (P_f), gravid females (P_g), adult males (P_m), and copepodites (P_c) that are plotted in Fig. 2. With this technique it is possible to derive negative population sizes, depending on the values of mean monthly population density, and it is necessary to adjust these values to zero or to apply some other correction.

Egg Development

The maximum potential production of eggs and their rate of recruitment into nauplii (R_{nmax}) was a function of the development time of eggs (Fig. 1), the population density of gravid females (Fig. 2a), and the mean number of eggs per gravid female which is estimated to be 19 (Coull and Dudley 1976) and is assumed constant, although we relaxed this assumption in one simulation and showed that seasonal variation in clutch size of between 15 and 24 per gravid female (Palmer 1980) has no significant effect on R_{nmax} or subsequent calculations (Fig. 3). Thus, the maximum potential egg maturation rate (R_{nmax}) is given by

(11) $R_{nmax}(t) = 19 \times P_g(t)/E(t)$

where $E(t)$ is the development time (days) of eggs on day t (from Eq. 1 and 4). For example, the total number of eggs in the population on day t is equivalent to $19 \times P_g(t)$, and if the development time is say 10 d, then on that day an average of 1/10 of the total number of eggs will develop into nauplii. This and subsequent equations were solved numerically using the time series of population densities that were generated by the procedure shown above.

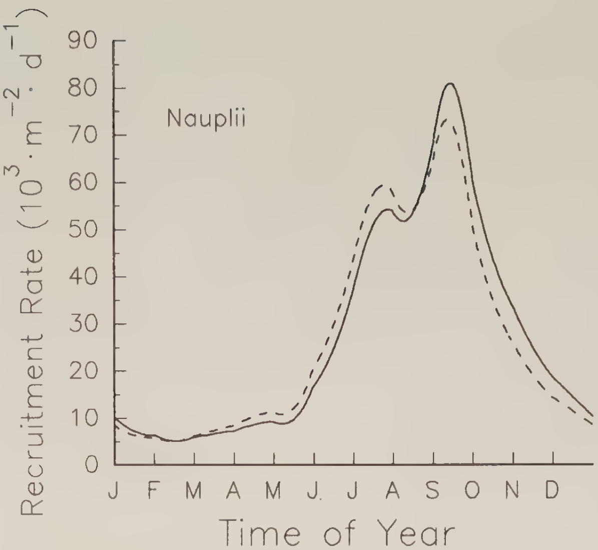


FIG. 3. Calculated rate of the maximum potential recruitment into the nauplii population (R_{nmax}) from Eq. 11 when clutch size was 19 per gravid female and constant (—) or seasonally variable between 15 in winter and 24 in May (---).

From Eq. 11, the maximum daily recruitment of nauplii is greatest from July through September (Fig. 3). This is largely due to the decrease in egg development time (Fig. 1) which is temperature dependent, as the number of gravid females during these summer months is fairly stable (Fig. 2a). Egg development time decreases from a maximum of 10 d in cold months (remember that *M. littorale* is gravid year-round) to a minimum of 2 d in the warmest months. This, and changes in the density of gravid females, gives potential naupliar recruitment rates that change seasonally from 5×10^3 to $81 \times 10^3 \cdot m^{-2} \cdot d^{-1}$ (Fig. 3). Neither the annual rate nor seasonality of recruitment changed significantly when clutch size was allowed to vary seasonally compared with simulations that assumed a constant clutch size (Fig. 3).

The summation of daily egg hatching rates gives an estimate of the potential production of the *Macroarthridion* population, within the limits set by the observed population size of gravid females (Fig. 2a). Potential production of nauplii by the observed population of gravid females is $10\,002 \times 10^3 \cdot m^{-2} \cdot yr^{-1}$ (Table 1). This is the maximum potential rate because it assumes zero mortality of eggs, and it demonstrates that the potential number of recruits into nauplii and later life stages is large. It also suggests that the mortality of nauplii must be massive, considering that the observed population size of copepodites (Fig. 2b) is about 3 orders of magnitude lower than the potential recruitment rate.

Maximum Adult Recruitment

The maximum rate at which copepodites may be recruited into the adult population (R_{amax}) is a function of the population size of copepodites (P_c) and their development (C):

(12) $R_{amax}(t) = P_c(t)/C(t)$.

This gives the maximum rate of adult recruitment because the calculations assume a uniform age distribution for copepodites.

TABLE 1. Model calculations of annual production for nauplii (ΣR_{nmax}), copepodites (ΣR_{cmin}), and adult *Microarthridion* (ΣR_{amax} and ΣG_{amin}) based on monthly mean population densities from the 17-yr data set.

Population parameters	Numerical production ($10^3 \cdot m^{-2} \cdot yr^{-1}$)	Individual dry weight (μg)[a]	Biomass production ($g \cdot m^{-2} \cdot yr^{-1}$)
Nauplii (maximum potential)	10 002	0.2	2.0
Copepodites (minimum)	147	0.5	0.07
Adults (maximum potential)	146	2.0	0.3
Adults (minimum)	38	2.0	0.08

[a] From Fleeger and Palmer (1982).

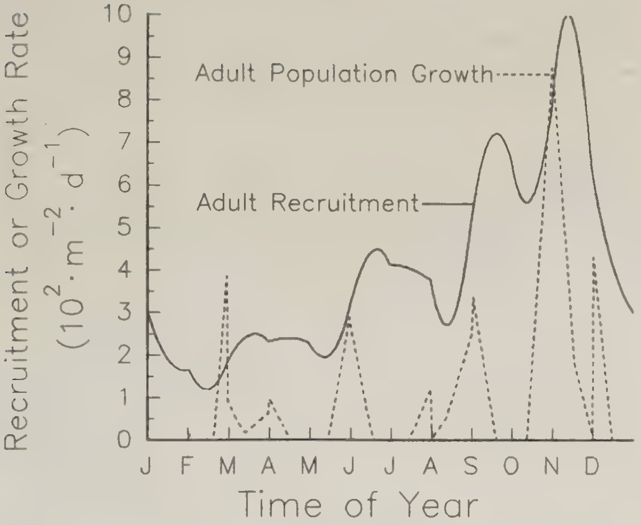


FIG. 4. Calculated rates of maximum potential recruitment into the adult population from maturing copepodites (—), R_{amax} from Eq. 12, and of the positive growth and minimum productivity of the total adult population (---), G_{amin} from Eq. 13.

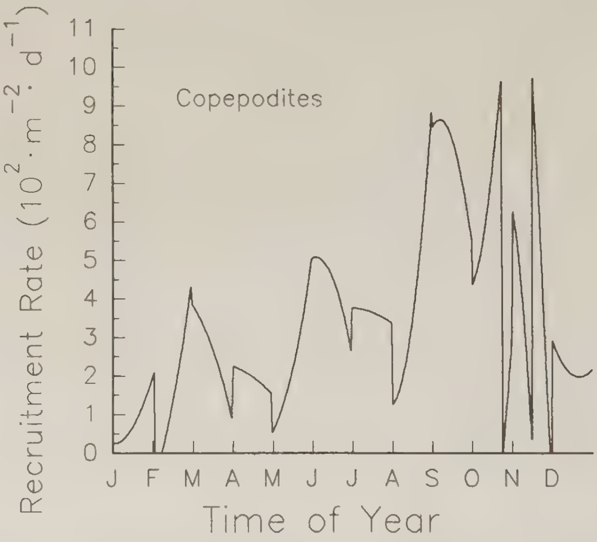


FIG. 5. Calculated minimum rate of recruitment into the copepodite population, R_{cmin} from Eq. 14a and 14b, that is required to maintain the population density at the observed levels.

Recruitment into the adult population (Fig. 4) varies seasonally between about 120 and $1000 \cdot m^{-2} \cdot d^{-1}$. But unlike potential egg development which shows one major peak annually, copepodite development shows three or four cycles annually, corresponding to the population cycles of copepodites (Fig. 2b). The amplitudes of adult recruitment cycles are either exaggerated or diminished by changes in copepodite development time which vary seasonally with temperature between 14 and 33 d (Fig. 1).

The integrated rate of adult recruitment, $146 \times 10^3 \cdot m^{-2} \cdot yr^{-1}$, provides a maximum estimate of the production of adult *Microarthridion*. This estimate assumes that there is zero mortality of copepodites and that all copepodites in the population reach the age of metamorphosis. From this calculation, we see that the potential production of adults has decreased from $10\,002 \times 10^3 \cdot m^{-2} \cdot yr^{-1}$, the potential rate of naupliar recruitment, to 1.5% of this value, i.e. $146 \times 10^3 \cdot m^{-2} \cdot yr^{-1}$ (Table 1).

Positive Adult Population Growth

The positive rate of adult population growth (G_{amin}) was calculated as the sum of positive increments in male (G_{am} in equations below) and female populations (G_{af}):

$$G_{af}(t) = P_f(t+1) - P_f(t) \text{ when } P_f(t+1) - P_f(t) > 0$$
$$G_{af}(t) = 0 \text{ when } P_f(t+1) - P_f(t) \leq 0$$

$$(13) \quad G_{am}(t) = P_m(t+1) - P_m(t) \text{ when } P_m(t+1) - P_m(t) > 0$$
$$G_{am}(t) = 0 \text{ when } P_m(t+1) - P_m(t) \leq 0$$
$$G_{amin}(t) = G_{af}(t) + G_{am}(t).$$

Results of this calculation are shown in Fig. 4. It is significant that, like adult recruitment, positive growth of the adult population shows four major peaks throughout the year, and these peaks correspond approximately to the times of maximum adult recruitment (Fig. 4). It should be noted that calculations of adult growth and recruitment are independent, and the probability that these cycles are real is increased greatly because they are positively correlated.

The minimum estimate of annual adult productivity was obtained by summing $G_{amin}(t)$. This is a minimum estimate because it does not account for the turnover of adults. The result of this calculation indicates that adult productivity is constrained between a minimum of $38 \times 10^3 \cdot m^{-2} \cdot yr^{-1}$ and a maximum, from the calculation of maximum recruitment, of $146 \times 10^3 \cdot m^{-2} \cdot yr^{-1}$.

Minimum Copepodite Recruitment and Mortality

The minimum recruitment into the copepodite population (R_{cmin}) necessary to maintain the population at the observed level is a function of the change in population density of copepodites and their development into adults. For example, if the copepodite population density is constant, then the minimum recruitment into the population must equal the rate of conver-

TABLE 2. Estimates of mean annual rates ($10^3 \cdot m^{-2} \cdot yr^{-1}$), computed from the monthly means of the 17-yr data set, of the maximum possible recruitment of nauplii (R_{nmax}), the minimum possible recruitment of nauplii into the copepodite population (R_{cmin}), the minimum mortality required of the copepodite population (M_{cmin}), and the maximum possible recruitment of copepodites into the adult population (R_{amax}) as a function of the annual mean temperature.

Population parameters	Annual mean temperature (°C)		
	17.5	19.5	21.5
R_{nmax}	8260	10 002	11 813
R_{cmin}	132	147	163
M_{cmin}	0.6	0.4	0.2
R_{amax}	132	146	162

sion into adults. If the copepodite population is rising, then their recruitment must equal the rate of increase plus the rate of conversion into adults. This was calculated as follows:

$$\text{(14a)}\quad R_{cmin}(t) = [P_c(t+1) - P_c(t)] + P_c(t)/C(t)$$

$$\text{when } \{[P_c(t+1) - P_c(t)] + P_c(t)/C(t)\} > 0$$

and

$$\text{(14b)}\quad R_{cmin}(t) = 0$$

$$\text{when } \{[P_c(t+1) - P_c(t)] + P_c(t)/C(t) < 0.$$

These calculations show that several major cycles of recruitment into the copepodite population (Fig. 5) are necessary to maintain the observed population.

Summation of $R_{cmin}(t)$ gives an estimate of the minimum annual productivity of copepodites which is $146.7 \times 10^3 \cdot m^{-2} \cdot yr^{-1}$. This is only slightly greater than the estimate of maximum adult recruitment, $R_{amax} = 146.4 \times 10^3 \cdot m^{-2} \cdot yr^{-1}$ (Table 1), and the difference of $371 \cdot m^{-2} \cdot yr^{-1}$ represents the mortality of copepodites that is required to maintain the observed population size.

The mortality rate (M_{cmin}) can also be computed directly as follows:

$$\text{(15a)}\quad M_{cmin}(t) = |[P_c(t+1) - P_c(t)]| - P_c(t)/C(t)$$

$$\text{when } |[P_c(t+1) - P_c(t)]| > P_c(t)/C(t)$$

$$\text{and } [P_c(t+1) - P_c(t)] < 0$$

and

$$\text{(15b)}\quad M_{cmin}(t) = 0$$

$$\text{when} [P_c(t+1) - P_c(t)] > 0$$

$$\text{or when } |[P_c(t+1) - P_c(t)]| < P_c(t)/C(t).$$

The logic of these equations is simply that there must be a source of mortality on the copepodite population when the population density is falling and when the rate of decrease is greater than that which can be accounted for by maturation. In that case, the mortality rate must equal the absolute value of the rate of population decline minus the maturation rate. Summation of $M_{cmin}(t)$ yields the same estimate of mortality as that given above.

TABLE 3. Estimates of annual rates ($10^3 \cdot m^{-2} \cdot yr^{-1}$), computed from a 5-yr series of monthly and biweekly (beginning 1981) data, of the maximum possible recruitment of nauplii (R_{nmax}), the minimum possible recruitment of nauplii into the copepodite population (R_{cmin}), the minimum mortality required of the copepodite population (M_{cmin}), the maximum possible recruitment of copepodites into the adult population (R_{amax}), and the minimum productivity of the adult population (G_{amin}).

Population parameters	Calendar year				
	1979	1980	1981	1982	1983
R_{nmax}	10 580	7591	6677	3092	12 745
R_{cmin}	145	130	109	128	226
M_{cmin}	11	20	40	40	70
R_{amax}	129	113	71	91	154
G_{amin}	53	83	72	78	133

Examination of the time series of M_{cmin} (data not shown) shows that only during portions of January, February, and November are there times when maturation alone cannot account for declining copepodite populations. It is interesting that changes in copepodite density can be accounted for almost entirely by recruitment into and out of the population with almost no mortality. That is, most of the behavior we observe in population density can be explained by periodic bursts of recruitment into the population followed by declining populations resulting from maturation. If recruitment into the population is greater, in reality, than our calculations of the minimum requirement, then mortality must rise by an equivalent amount in order to maintain the population at the observed levels.

Temperature Dependence

Several simulations were made in which the mean annual water temperature was varied between 17.5 and 21.5°C. These results indicated that the potential production of *Microarthridion* increases considerably, and exponentially, with temperature (Table 2), provided that the population of gravid females does not decrease below observed levels as temperature increases. The average slope of the response of R_{nmax}, the maximum potential recruitment of nauplii, between 17.5 and 21.5°C is 888×10^3 per degree which is equivalent to a 9% increase in potential production per degree rise in mean annual temperature. This demonstrates the extreme sensitivity of egg production and development to temperature, and it suggests that interannual and seasonal temperature changes are quite important to the population dynamics of *Microarthridion*.

Other rate calculations are also temperature sensitive. For example, calculations of the required minimum number of recruits into the copepodite population (R_{cmin}) and of maximum adult recruitment (R_{amax}) also increase with temperature (Table 2) because of the sensitivity of these calculations to development times. These indicate simply that the turnover of individuals in the population must increase, if development times decrease and population densities remain unchanged. Estimates of the mortality required of the copepodite population (M_{cmin}) decrease with increasing temperature because the maturation rate, which increases with temperature, can account for a greater share of the periodic declines in copepodite density.

Temporal Variation

To examine interannual variability and to investigate the effects on model calculations of temporal variability in the population data, we solved the model equations using the raw time series of population data from 1979 to 1983 inclusive. Interannual variation in temperature was held to zero; the parameters in Eq. 4 were kept constant, so any interannual variation in the calculations of recruitment is due to variation in the population data rather than to changes in the temperature-dependent development times. The results demonstrate that interannual variability is high in all estimates of recruitment and production (Table 3). For example, maximum annual recruitment of nauplii (R_{nmax}) ranged between a low of 3092 × $10^3 \cdot m^{-2}$ in 1982 to a high of 12 745 × $10^3 \cdot m^{-2}$ in 1983. All other estimates of recruitment and mortality varied annually by about a factor of 2. In 1983, the year of greatest potential nauplius recruitment, we also saw the greatest copepodite mortality (M_{cmin}), adult population growth (G_{amin}), recruitment of adults (R_{amax}), and recruitment of copepodites (R_{cmin}) (Table 3).

Discussion

Since growth and reproduction in all stages of *M. littorale* are dependent on temperature (Eq. 1, 2, and 3), why are the in situ population densities not greatest in summer rather than in autumn/winter (Fig. 2)? According to our simulation the population certainly has the ability to achieve a much larger density than we have observed during the warmer months, yet it does not do so. *Microarthridion littorale* is an epibenthic copepod living right at the sediment water interface in the upper 3 mm of sediment (Fleeger 1979), and as such is susceptible to predation by a suite of bottom feeding fishes, particularly by juvenile spot (*Leiostomus xanthurus*). Yearly, millions of larval spot enter the North Inlet estuary in January. By the end of March the pelagic feeding larvae metamorphose into bottom-feeding juveniles (about 20 mm) which feed almost exclusively on epibenthic meiobenthic copepods (Smith and Coull 1987; Ellis and Coull 1989; Nelson and Coull 1989; Coull 1990; Feller et al. 1990). They continue to feed on the meiobenthos throughout the spring and summer, when by late August/September they have grown to >60 mm and feed primarily on benthic macrofauna (polychaetes, amphipods, bivalve siphons, shrimp, etc.). These large numbers of spot along with several other benthic feeding fish have long been suspected (see Fleeger 1979) of significantly impacting the epibenthic copepod population. *Microarthridion* is the dominant epibenthic species in the system and comprises most of the gut contents of juvenile spot (Feller et al. 1990).

Attempts to estimate the potential predation impact on field population dynamics have not been very successful because the fish localize their feeding activity (they school) but, more importantly, meiobenthic copepods are highly patchy in the field (Hicks and Coull 1983). Variance associated with quantitative meiofaunal collections after predation by the fish has been so great that the impact, particularly stage-specific mortality (see Ellis and Coull 1989), has been masked by large sampling errors. The simulations, however, clearly demonstrate a tremendous mortality of *M. littorale* from egg to adult and that most of the mortality is associated with the naupliar or egg stages (Table 1). Because the North Inlet copepod fauna is not monospecific, none of the previous predation/meiofauna studies have been able to assess naupliar mortality due to predation. In New Zealand, Hicks (1984), working with a field population of copepods where one species with distinctive nauplii comprised 98.6% of the total copepod assemblage, clearly demonstrated that juvenile flatfishes preferentially preyed on nauplii. He concluded, however, that such predation had little impact on the ultimate population size of the copepod.

Could it be that our *M. littorale* population does not peak when it should based on temperature because most of the in situ mortality occurs in the naupliar stages (as our model predicts)? We do not know if juvenile spot preferentially prey on *Microarthridion* nauplii as the New Zealand flatfishes did on *Parastenhelia megarostrum* (Hicks 1984). Is the predation pressure so great during March–September that it is only when the spot grow to the stage where they feed on macrobenthos (release predation pressure on meiobenthic copepods) that *M. littorale* is able to expand its population size? We fully believe this to be the case (or we have to invent another source of naupliar mortality). Thus, *Microarthridion* does not reach its maximum population size at the optimum temperature, and predation appears to have a profound impact on the population dynamics of a meiobenthic species, a concept heretofore denied (Alheit and Scheibel 1982; Hicks 1984; Gee 1987) or under debate (Gee 1989; Coull 1990).

Is there any logic to the four cycles of copepodite and adult growth (Fig. 4 and 5)? These cycles are unrelated (in terms of model calculations) to changes in density of gravid females because the behavior of maximum potential naupliar recruitment (Fig. 3) is entirely different from that of adult recruitment and growth (Fig. 4). In several harpacticoid copepods including *M. littorale*, a significant fraction of nauplii can delay development and assume a state of "dormancy" (Coull and Dudley 1976). If there are periodic environmental cues that promote this behavior, such that a portion of the nauplier population delays development and avoids almost certain mortality, then this could produce the cyclic behavior that we observe. Or there may be periodic waves of predators, different fish species perhaps, that enter the estuary at different times of year.

It also appears that there are reversals in positive, adult population growth that precede peaks in adult recruitment (Fig. 4). This may indicate that there are periodic waves of adult mortality that coincide with adult recruitment. If true, then we would predict that the maximum life span of adult *M. littorale* is about 3 mo in the field because there are four growth cycles per year. Furthermore, it is tempting to speculate that these growth cycles correspond to four synchronous generations annually. However, this seems unlikely because the generation time (Fig. 1) from egg to egg is considerably shorter than 3 mo.

In general, calculations of productivity that are based on summations of the positive growth of population density increase as the frequencies and ranges of population cycles increase, i.e. as temporal variability increases. However, estimates of recruitment into the copepodite population (R_{cmin}) did not differ between the averaged and raw data (Tables 1 and 3, respectively), and estimates of adult recruitment (G_{amin}) increased only slightly when raw data were used in the simulations. This indicates that averaging of the 17-yr record of copepodite and adult densities did not remove an excessive amount of intraannual variation, real or otherwise.

All population parameters investigated tended to covary in simulations of the 5-yr time series of raw data (Table 3). For example, 1983 had the highest rates of recruitment and mortality in all population stages (Table 3). Because the calculations of recruitment, mortality, and production for the different populations are independent, we would expect no covariation among interannual estimates of recruitment into the different populations if the intraannual variability in estimates of population density were greatly inflated by sampling error. Therefore, the interannual variability in the estimates of population parameters (Table 3) is probably accurate. Fleeger and Palmer (1982) also observed significant (100%) variability in annual adult productivity. Furthermore, the magnitude of interannual variability (Table 3) is actually greater than that expected from temperature changes of 4°C (Table 2), which suggests that predation or other factors may regulate temporal changes in population density.

Given the large number of potential recruits into the naupliar population, population control is most likely from predation as reasoned above. The combined mortality of eggs and nauplii could be as great as 98% and there would still be sufficient recruitment to maintain the observed copepodite population (Table 1). However, as there are no estimates of nauplii densities, we cannot make a conclusion about the absolute control of copepodite populations. At the adult life stage, the estimate of minimal productivity was 26% of the maximum potential adult recruitment (Table 1), which suggests that recruitment into the adult population is largely responsible for the size and dynamics of that population. The close agreement between cycles of positive adult growth and maximum recruitment into that population (Fig. 4) supports this conclusion. Thus it appears to be naupliar mortality that limits the population size of *M. littorale* in North Inlet, South Carolina, and this naupliar mortality is most likely the result of juvenile fish predation.

Estimates were made of the biomass production of each life stage, including nauplii, a frequently neglected component of previous meiobenthic copepod production studies (Feller and Warwick 1988). Even though the weight of an individual nauplius is about 10% that of an adult (Fleeger and Palmer 1982), the potential biomass production of nauplii still greatly exceeds that of adults and copepodites combined (Table 1). Our calculations of productivity exceed those made by Fleeger and Palmer (1982) who estimated productivity of *M. littorale* at an intertidal site at North Inlet by a method that computes the growth rates of all individuals in a population, and so provides an estimate of the instantaneous growth of the extant population but does not include the turnover rate of individuals. Our model predictions of maximum potential production account for turnover, and the estimated $0.2\ \mathrm{g \cdot m^{-2} \cdot yr^{-1}}$ maximum production for the adult population exceeds that of Fleeger and Palmer ($0.04\ \mathrm{g \cdot m^{-2} \cdot yr^{-1}}$, calculated from their data) by a factor of 5. Our estimate of the minimum copepodite production of $0.07\ \mathrm{g \cdot m^{-2} \cdot yr^{-1}}$ is similar to the Fleeger and Palmer estimate of about $0.05\ \mathrm{g \cdot m^{-2} \cdot yr^{-1}}$. But their estimate of nauplii production, also about $0.05\ \mathrm{g \cdot m^{-2} \cdot yr^{-1}}$, is considerably less than our calculation of the maximum potential production of $2.0\ \mathrm{g \cdot m^{-2} \cdot yr^{-1}}$ (Table 1), which supports our conclusion that mortality (turnover) of the nauplii population controls the population dynamics of *M. littorale*.

Even though *M. littorale* constitutes about 80% of the gut contents of starry flounder (*Platichtys stellatus*) of <25 mm standard length in Alaska (J. McCall, pers. comm.) and about 50% of the total copepods in the guts of juvenile spot from North Inlet (Feller et al. 1990, from their fig. 4), with a maximum potential biomass production of about $2.0\ \mathrm{g \cdot m^{-2} \cdot yr^{-1}}$ (Table 1), one has to question if *M. littorale* is an important source of calories for its fish predators. This production value is consistent also with estimates made for other harpacticoid copepods (Feller 1982; Herman et al. 1984).

Several lines of information suggest that harpacticoids may be a necessary dietary component for many juvenile fishes. When juvenile chum salmon (*Oncorhynchus keta*) were fed an amphipod, a calanoid copepod, and the harpacticoid *Tigriopus californicus*, the food conversion efficiency of the salmon was twice as high (40%) on the harpacticoid, even though *Tigriopus* was fed at half the ration of the amphipod and calanoid (Volk et al. 1984). Additionally, harpacticoid copepods are naturally rich in the 20:5ω3 and 22:6ω3 fatty acids required to promote growth in marine fishes (Watanabe et al. 1983). Thus the predominance of harpacticoids in the guts of many fish may be a consequence of more than simple caloric intake. However, we would argue that it is unlikely that benthic copepods, of which *M. littorale* accounts for 18% of total numbers at North Inlet (Coull and Dudley 1985), represent a major source of calories to the fish that frequent the North Inlet estuary.

Acknowledgment

This research was supported by the Biological Oceanography Program of NSF (OCE85-21345 and OCE89-16255, B.C.C. principal investigator) and NSF's Long Term Ecological Research Program (BSR 9011664, F. J. Vernberg principal investigator). Modeling and data analyses were completed during a sabbatical leave by J.T.M. to the Botansk Institute, Aarhus University. Special thanks to Bettye W. Dudley who sorted the meiofaunal samples. We appreciate the effort and suggestions made by two anonymous reviewers.

References

ALHEIT, J., AND W. SCHEIBEL. 1982. Benthic harpacticoids as a food source for fish. Mar. Biol. 70: 141–147.

COULL, B. C. 1990. Are members of the meiofauna food for higher trophic levels? Trans. Am. Microsc. Soc. 109: 233–246.

COULL, B. C., S. S. BELL, A M. SAVORY, AND B. W. DUDLEY. 1979. Zonation of meiobenthic copepods in a Southeastern United States salt march. Estuarine Coastal Mar. Sci. 9: 181–188.

COULL, B. C., AND B. W. DUDLEY. 1976. Delayed naupliar development of meiobenthic copepods. Biol. Bull. (Woods Hole) 150: 38–46.

1985. Dynamics of meiobenthic copepod populations: a long-term study (1973–1983). Mar. Ecol. Prog. Ser. 24: 219–229.

COULL, B. C., AND R. J. FELLER. 1988. Site-to-site variability in abundance of meiobenthic copepods along a tidal gradient over 24 hours. Hydrobiologia 167/168: 477–483.

COULL, B. C., AND W. B. VERNBERG. 1975. Reproductive periodicity of meiobenthic copepods: seasonal or continuous? Mar. Biol. 32: 289–293.

ELLIS, M. J., AND B. C. COULL. 1989. Fish predation on meiobenthos: field experiments with juvenile spot *Leiostomus xanthurus* Lacepede. J. Exp. Mar. Biol. Ecol. 130: 19–32.

FELLER, R. J. 1982. Empirical estimates of carbon production for a meiobenthic harpacticoid copepod. Can. J. Fish. Aquat. Sci. 39: 1435–1443.

FELLER, R. J., B. C. COULL, AND B. T. HENTSCHEL. 1990. Meiobenthic copepods: tracers of where juvenile *Leiostomus xanthurus* (Pisces) feed? Can. J. Fish. Aquat. Sci. 47: 1913–1919.

FELLER, R. J., AND R. M. WARWICK. 1988. Energetics, p. 181–196. *In* R. P. Higgins and H. Thiel [ed.] Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC.

FLEEGER, J. W. 1979. Population dynamics of three estuarine meiobenthic harpacticoids (Copepoda) in South Carolina. Mar. Biol. 52: 147–156.

FLEEGER, J. W., AND M. A. PALMER. 1982. Secondary production of a meiobenthic copepod, *Microarthridion littorale*. Mar. Ecol. Prog. Ser. 7: 157–162.

GEE, J. M. 1987. Impact of epibenthic predation on estuarine intertidal harpacticoid copepod populations. Mar. Biol. 96: 497–510.

1989. An ecological and economic review of meiofauna as food for fish. Zool. J. Linn. Soc. 96: 243–261.

HERMAN, P. M. J., C. HELP, AND B. GUILLEMIJN. 1984. Production of *Tachidius discipes* (Copepoda: Harpacticoida). Mar. Ecol. Prog. Ser. 17: 271–278.

HICKS, G. R. F. 1979. Pattern and strategy in the reproductive cycles of benthic harpacticoid copepods, p. 139–147. *In* E. Naylor and R. G. Hartnoll [ed.] Cyclic phenomena in marine plants and animals, Proc. 13th European Marine Biology Symposium. EDS. Pergamon Press, Oxford, UK.

1984. Spatio-temporal dynamics of a meiobenthic copepod and the impact of predation-disturbance. J. Exp. Mar. Biol. Ecol. 81: 47–72.

HICKS, G. R. G., AND B. C. COULL. 1983. The ecology of marine meiobenthic harpacticoid copepods. Oceanogr. Mar. Biol. Annu. Rev. 21: 67–175.

NELSON, A. L., AND B. C. COULL. 1989. Selection of meiobenthic prey by juvenile spot (Pisces): an experimental study. Mar. Ecol. Prog. Ser. 53: 51–57.

PALMER, M. A. 1980. Variation in life-history pattern between intertidal and subtidal populations of the meiobenthic copepod *Microarthridion littorale*. Mar. Biol. 60: 159–160.

PALMER, M. A., AND R. R. BRANDT. 1981. Tidal variation in the sediment densities of marine benthic copepods. Mar. Ecol. Prog. Ser. 4: 207–212.

PALMER, M. A., AND B. C. COULL. 1980. The prediction of development rate and the effect of temperature for the meiobenthic copepod *Microarthridion littorale* (Poppe). J. Exp. Mar. Biol. Ecol. 48: 73–83.

SMITH, L. D., AND B. C. COULL. 1987. Juvenile spot (Pisces) and grass shrimp predation on meiobenthos in muddy and sandy substrata. J. Exp. Mar. Biol. Ecol. 105: 123–136.

VOLK, E. C., R. C. WISSMAR, C. A. SIMENSTAD, AND D. M. EGGERS. 1984. Relationship between otolith microstructure and growth of juvenile chum salmon *Oncorhynchus keta* under different prey rations. Can. J. Fish. Aquat. Sci. 41: 126–133.

WATANABE, T. C., C. KITAJAMA, AND S. FUJITA. 1983. Nutritional values of live organisms used in Japan for mass propagation of fish: a review. Aquaculture 34: 115–143.

Colonization by Lotic Macroinvertebrates: A Review of Processes and Patterns

Rosemary J. Mackay

Department of Zoology, University of Toronto, Toronto, Ont. M5S 1A1, Canada

Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Can. J. Fish. Aquat. Sci. 49: 617–628.

Ways in which invertebrates colonize lotic habitats are reviewed, tracing patterns in behaviour, trophic ecology, and life history that could lead to predictions concerning resilience of stream communities after disturbance. Patterns are described for small-scale experimental studies using introduced or natural substrates, for large-scale observations of new or rewatered channels, for rivers recovering from pollution, and for unstable rivers with fluctuating discharge. Colonization depends on invertebrate mobility (drift, swimming, crawling, and flight), substrate texture and associated food supplies, competition, and predation. Epilithon-browsers and filter feeders can use the resources of smooth stones; gatherers colonize as fine detritus accumulates; grazers increase as periphyton becomes established; shredders and predators tend to be late arrivals. Propagules for colonization are made more available by asynchronous and aseasonal life cycles, long oviposition periods, and refuges in the streambed or neighbouring waterbodies. Species in frequently disturbed streams benefit from these characteristics. Although disturbance may be due to stochastic factors, recovery is not due to chance. Recurring ecological patterns among early colonizers suggest that knowledge of the hydrologic regime, food resources, and dominant taxa can be used to predict the overall resilience of a stream community.

L'auteur examine les diverses manières dont les invertébrés colonisent les habitats lotiques en établissant les schèmes de comportement, l'écologie trophique et les cycles de vie qui pourraient permettre de prévoir la capacité de rétablissement des communautés des eaux courantes après qu'elles aient été perturbées. Il décrit les régimes établis lors d'expériences à petite échelle à partir de substrats nouveaux ou naturels, d'observations à grande échelle de nouveaux et d'anciens lits, ainsi que d'études de rivières après leur pollution et de rivières instables à débit irrégulier. La colonisation dépend de la mobilité des invertébrés (dérive, nage, reptation et vol), la texture du substrat et les ressources alimentaires qu'il contient, la compétition et la prédation. Les brouteurs d'épilithon et les filtreurs peuvent se nourrir à même les pierres lisses; les récolteurs s'établissent au fur et à mesure que les détritus fins s'accumulent; l'abondance des brouteurs augmente en fonction de la croissance du périphyton tandis que les prédateurs et les déchiqueteurs tendent à s'implanter en dernier. La colonisation par propagules est favorisée par des cycles de vie asynchrones et non saisonniers, de longues périodes d'oviposition et le refuge dans le lit du cours d'eau ou des bassins avoisinants. Les espèces peuplant des cours d'eau fréquemment perturbés bénéficient de ces caractéristiques. Quoique les perturbations peuvent être le résultat de facteurs stochastiques, le rétablissement ne se fait pas au hasard. Des schèmes écologiques récurrents observés chez les premiers colonisateurs portent à croire qu'une connaissance du régime hydrologique, des ressources alimentaires et des taxons dominants peut permettre de prévoir la capacité de rétablissement d'une communauté lotique.

Received July 9, 1990
Accepted October 4, 1991
(JA640)

Reçu le 9 juillet 1990
Accepté le 4 octobre 1991

1. Introduction

Streambeds providing the basic habitat of lotic invertebrates are variously exposed to the forces of flowing water and, in certain climates, to drought. Because most invertebrate species are mobile or sedentary rather than sessile, many individuals are displaced during periods of high discharge when rocks may be scoured, overturned, or rolled downstream, and finer streambed substrates are stirred or shifted. Even moderate variations in flow often result in unoccupied patches of substrate. At the other extreme, drought may temporarily bare the entire streambed. In spite of such disturbances to their environment, benthic invertebrates are diverse and abundant in unpolluted running water. How do populations reestablish themselves?

According to theories developed by MacArthur and Wilson (1967), a superior colonizer in an uncrowded environment has an advantage due to its high rate of population growth. Associated characteristics are small body size, semelparity, and short life span (Pianka 1970). These traits are shared by most stream-living macroinvertebrates (although many molluscs are exceptions); and if true to theory, at least the arthropods dominating lotic benthic assemblages should be good colonizers. They are, of course, in the sense that they maintain populations in the often-uncertain habitat of a stream. However, as this review will demonstrate, some taxa are faster colonizers than others and share features of life history and trophic ecology that give them additional advantages in the early stages of community development.

The purpose of this review is (1) to trace patterns of colonizing ability that are evident from descriptive and experimental studies in many different streams and (2) to show that these patterns have predictive value which may be used to assess the potential resilience of streams exposed or vulnerable to unnatural disturbance. The emphasis is on insects because more information on them is available.

The need to find ways of predicting responses to disturbance is particularly urgent in the case of streams and rivers because benthic habitats are often disrupted indirectly by practices and pollutants in surrounding catchments. May (1984) doubted that any multispecies community was sufficiently well understood for confident predictions to be made about its response to disturbance. But he also acknowledged that practical decisions on environmental matters often have to be made in spite of imperfections in our knowledge. Tentative generalizations or patterns are a first step in developing guidelines for practical management problems. Moreover, the detection of natural patterns is the mission of community ecology (Wiens 1984) and forms the basis for hypotheses to explain the processes causing patterns.

In the last decade, ecologists in general have come to realize that disturbance may play an influential role in community dynamics (Sousa 1984; Strong et al. 1984). Thus, stream communities disturbed by highly variable discharge, for example, like many in Australia and New Zealand, would be kept in a nonequilibrium state and prevented from achieving ecological saturation and tight species packing, which theoretically should characterize a stable, resource-limited and niche-controlled structure (Resh et al. 1988; Townsend 1989).

A disturbed stream, then, has not been seen merely as a practical problem to be tackled by applied ecologists. A disturbance, either real or simulated, has also enabled more basic stream ecologists to explore theories on island biogeography and the relative importance of stochastic and deterministic processes in shaping community structure. As a result, a large body of literature has developed on the rates at which bare patches of stream substrate, both large and small, are colonized by invertebrates. Studies of recovery following disturbance have shown or suggested the colonization mechanisms responsible for restoring a community to its predisturbance state. Gore and Milner (1990) and Wallace (1990) reviewed many of these mechanisms, and Sheldon (1984) and Gore and Milner (1990) discussed some numerical responses of colonizing aquatic insects. No review, however, has looked for correlations between named colonizing taxa, their ecological characteristics, and the types of streams they inhabit. This review considers how, and under what environmental influences, invertebrates colonize newly available space at four different scales: small bare patches, denuded reaches, new or rewatered channels, and broadly disturbed streams. Characteristics common to early or late colonizers are examined for patterns that might lead to predictions for recovery following disturbance.

2. Colonization Scales and Mechanisms

Spatial and temporal scales of colonization range from biogeographic to extremely local and immediate phenomena. Vivid examples in running waters were given by Sheldon (1984). The scale of most experimental work in streams has been small (<1 m^2 of streambed) and has documented the establishment of macroinvertebrate assemblages following a variety of treatments that ensured an initial absence, or lowered density, of organisms. A recurring theme in such studies has been the MacArthur–Wilson model of island colonization, the islands being the bared stones or patches of substrate (or introduced substitutes) (Gore and Milner 1990). It is arguable whether such an approach is a proper use of the model given that (1) the original theory was developed for species breeding on islands whereas residency in stream patches is transitory, (2) stream ''islands'' are not surrounded by a foreign and inhospitable ''sea'', and (3) the species pool equivalent to the model's mainland, which is the source of colonizers, is usually the immediately adjacent streambed. The island situation does not even resemble the modified scenario of Simberloff (1974). In spite of their imperfections in terms of the MacArthur–Wilson model, however, small-scale studies of colonization have resulted in valuable information on the mobility of lotic macroinvertebrates and their particular responses to bare patches of substrate.

Investigations of bare streambeds on a larger scale, as in a newly made stream channel, are rare; but streams exposed to severe disturbance have received more attention and share many of the drawbacks facing colonizers. A new channel with no previous inhabitants relies on somewhat distant sources for immigrants. Streams recovering from spates, drought, or unnatural chemical inputs may likewise depend on distant sources of colonizers but sometimes retain a few species or individuals in an unaffected refuge or life history stage.

Whatever the scale or cause of the uninhabited area of streambed, colonizers may reach a restored habitat in one or more ways: drifting (in the water) from upstream sources, crawling or swimming from adjacent substrates, including the hyporheic habitat, hatching from eggs laid near, on, or in the water, or flying in (amphibious bugs and beetles) and resuming an aquatic existence (Williams and Hynes 1976). Both the method and the timing of immigration by particular organisms depend on specific traits expressed in behaviour and life cycles that cause or allow a certain pattern.

3. Factors Affecting Colonization of Small Patches

3.1. Mobility of Invertebrates

Bare substrates placed in a stream have been shown to house invertebrates within 24 h, even when the substrates beforehand had been thoroughly dry or acid-scoured (and thus without epilithic growths) rather than merely brushed free of fauna (e.g. Wise and Molles 1979; Ciborowski and Clifford 1984; Lake and Doeg 1985; Boulton et al. 1988; Doeg et al. 1989b). Such rapid occupation of empty habitat shows that certain stream dwellers are extremely mobile. Some of these early arrivers may merely inspect the substrate during the course of their normal widespread foraging, and then depart just as rapidly (Giller and Cambell 1989). More sedentary organisms may be true colonizers in that they remain in the habitat until some other factor removes them or stimulates their departure some days or weeks later. Only net numerical change, rather than actual immigration and emigration, has been followed in most colonization studies; but some taxa increase in density sooner than others, reflecting both their own activity and the means by which propagules arrived.

3.1.1. Drift

When introduced substrates have been positioned to allow access from only certain sources (drift, adjacent natural substrates, air), drift seems to have provided most of the immigrants (Townsend and Hildrew 1976; Williams and Hynes 1976; Bird and Hynes 1981; Benson and Pearson 1987). Certainly those taxa most often listed among the earliest arrivals on bare substrates, such as Baetidae, *Gammarus*, Simuliidae, and Chironomidae (e.g. Waters 1964; Ulfstrand et al. 1974; Hynes

1975; Gray and Fisher 1981; Lake and Doeg 1985; Malmqvist and Otto 1987; Dudley 1988), are also known to be prominent in the drift (Waters 1972). However, Doeg et al. (1989b) found that drift contributed less than 50% of immigrants over 10 d, and they noted that the design of some substrate-holding trays hindered accessibility by crawling invertebrates in the surrounding streambed, resulting in overestimates of drift in these cases.

Minshall and Petersen (1985) claimed that drift was the primary means of redistribution of benthic organisms in streams. It is a particularly important relocating mechanism for invertebrates that do not move far under their own power such as the relatively sedentary filter-feeding caddisflies, black flies, and chironomids. Also, as discussed later with respect to large-scale events, drift from upstream reaches undoubtedly allows many taxa to recolonize disturbed reaches far downstream. Recent research employing direct observations of small patches, however, suggests that many of the extremely mobile invertebrates swim and crawl in all directions as well as drifting (Hart and Resh 1980; Wiley and Kohler 1981; Kohler 1984, 1985; Richards and Minshall 1988; Kohler and McPeek 1989).

3.1.2. Swimming

The vigorous swimming of Baetidae, Siphlonuridae, and some Oligoneuriidae is familiar to anyone who has tried to pick these mayfly larvae from a live sample of stream benthos. *Gammarus* is also a strong swimmer in sheltered water, and even in riffles can use deadwater areas downstream from rocks to scuttle across a stream (Hynes 1970). Some leptophlebiid mayfly larvae swim considerable distances upstream at certain times in their life cycles (Hayden and Clifford 1974; Söderström 1987).

Swimming down to the substrate allows some drifters to leave the water column deliberately, as seen in *Baetis* and *Gammarus* (Ciborowski and Corkum 1980). Mayfly larvae use dorsoventral undulations to swim downwards, and reach the bottom far sooner than stonefly and caddisfly larvae, probably because the hair-fringed cerci form an effective paddle (Otto and Sjöström 1985). Therefore the rapidity with which many mayflies and other lotic invertebrates reach local bare substrates may be due partly to drift and partly to their swimming, either from place to place on the substrate or when leaving the drift.

Doeg et al. (1989b) inferred that swimmers were important colonizers of experimental trays of sandy substrates in slow water that were raised above the streambed and out of reach of crawlers. Although these trays could have been colonized by drift (e.g. Ciborowski (1987) has shown that drifting *Baetis* larvae are transported laterally to slow water at stream margins), the taxonomic composition of drift (collected in a drift net) in this study was different from the fauna colonizing sand.

3.1.3. Crawling

Nearly all benthic macroinvertebrates can crawl, and some do so rapidly. Giller and Cambell (1989) concluded that crawling contributed as many mayflies to the colonization of implanted natural substrate trays as drift did, and that six species of the eight mayflies in the stream reached the trays only by crawling.

The mobility of grazers has attracted particular interest because their food resources, at least in the form of algal periphyton, can be quantified. Kohler (1984, 1985) showed that the direction and extent of movement by *Baetis* were related to periphyton levels. When the quantity of algal food was low, *Baetis* larvae moved more quickly and turned more often as they searched for a food-rich patch. Highly mobile grazers are able to cope with the patchy distribution of periphyton and find rare but preferred food items (Hart and Resh 1980; Hart 1981). Richards and Minshall (1988) estimated that 40–50% of *Baetis* larvae arriving on a single rock reached it by crawling. Ciborowski (1987) proposed that *Baetis* larvae settling out from the drift in marginal areas continued their search for food by crawling back towards periphyton in faster water.

After studying sources of colonization in a Sri Lankan river, Benzie (1984) concluded that all immigration resulted from random foraging activities over short distances. On a small scale, therefore, crawlers could colonize bare patches as effectively as drifters and swimmers.

3.1.4. Flight

At appropriate seasons, small patches of stream substrate may be colonized by flying (adult) insects. Amphibious adults (beetles and bugs) may fly in and remain. Nonaquatic adults may enter the water partly or completely to attach their eggs to submerged objects; others drop their eggs above water that provides appropriate cues. Some adults oviposit on banks or dry streambeds, providing a source of colonizers after drought. Oviposition is a means of rapid colonization, but adult activity and numbers of eggs per unit area of substrate are seldom documented.

The most important colonizing attribute of winged adults is their mobility which, together with appropriate sensory systems, allows them to search for suitable habitats. Moreover, some ovipositing adults are attracted to clean smooth substrates (Deutsch 1984; Imhof and Smith 1979) such as those often used or deliberately created for small-scale studies. Extensive oviposition was recorded on substrate trays placed in a desert stream after scouring spates in winter and summer (Gray and Fisher 1981). Total aerial colonization, including nonreproductive adults, accounted for two thirds of the taxa recolonizing the desert stream. Several species with long flight periods, and one that was iteroparous, ensured that adults could remain in the terrestrial environment until stream conditions became suitable, and that colonization could occur during most of the year (Gray 1981). In a long-term study where substrate baskets were introduced each month, Williams (1980) recorded several instances of mass colonization by first-instar larvae. He attributed their arrival to drift; however, larvae could have developed from eggs laid directly on the substrates, and an origin from egg clusters would explain the conspicuously clumped distribution of larvae.

3.2. Substrate Texture and Food

When small patches of substrate are physically disturbed, or when substrates are treated to mimic the disturbance effects, the factors most often described as having an influence on subsequent colonizers are changes in substrate texture and in the food resources associated either with the substrates themselves or with their arrangement on the streambed. As food materials and food gathering are difficult to separate from attributes of the substrate, they will be considered together.

3.2.1. Surface characteristics of substrates

Mild disturbance, such as turning a rock upside down, has little effect on grazers like baetids and glossosomatids, which will graze on periphyton on the under surface of a rock, as long as it fulfills their nutritional needs (Boulton et al. 1988). Heptageniids quickly move from one side of a stone to another and graze upper and lower surfaces (B. A. Heise, University of Toronto, Toronto, Ont., pers. comm.). Grazers depending on well lit periphyton "lawns," like *Leucotrichia*, are more severely affected (McAuliffe 1984), as are sedentary filter feeders in unsuitable below-stone currents (Boulton et al. 1988). Some of these organisms may move to the upper surface if the texture is suitable, but others are unable to change their positions (McAuliffe 1984). By turning rocks over at different intervals, Robinson and Minshall (1986) maintained periphyton biomass at low levels and found that invertebrate density and species richness were reduced as disturbance frequency increased. Therefore, this kind of tumbling has a negative effect on the community as a whole, but some invertebrates can feed on any rock surface or move to the preferred one.

When disturbance is severe, resulting in the scouring of epilithon and loss of trapped detritus and invertebrates, the substrates at first offer colonizers only attachement sites and shelter. Simuliidae larvae are known to avoid substrates covered with detritus, algae, or slime and to select smooth surfaces for attachment (Chutter 1968; Gersabeck and Merritt 1979; Ciborowski and Clifford 1984; Dudley et al. 1986; Morin 1987; Hershey and Hiltner 1988; Doeg et al. 1989b). Because these larvae are filter feeders, and hence independent of food materials growing on the substrates, they can take early advantage of unoccupied space.

Hydropsychid caddisflies are among insects favouring smooth clean surfaces for oviposition. They normally lay their eggs on smooth undersides of rocks that are free of silt (personal observations) and readily respond to substitutes in the form of acrylic tiles (Deutsch 1984) or hardboard (masonite) plates (e.g. Beckett and Miller 1982). Some Simuliidae behave in a similar way (Imhof and Smith 1979). Therefore, bare patches may attract ovipositing insects at appropriate seasons even if the actual propagules are not immediately obvious.

Bare stones soon become covered with organic layers, including a polysaccharide slime produced by colonizing bacteria (Geesey et al. 1978; Rounick and Winterbourn 1983). It is possible that the dissolved organic matter adsorbed onto stones provides a source of nutrients even before bacterial colonization because Winterbourn et al. (1985) found that *Baetis* spp. removed material from ashed stones without a detectable organic layer; and another species of *Baetis* rapidly colonized stones that had been acid-scoured by Boulton et al. (1988). This behaviour suggests that at least some species of *Baetis* are adapted for removing the thinnest of epilithic films, and can thus feed like browsers before the development of an algal layer. "Browsers" is a term used for invertebrates feeding on the organic layers of stones in New Zealand streams (Rounick and Winterbourn 1983). As fine epilithic detritus begins to accumulate, gatherers are provided with recognizable food (Madsen 1972; Calow 1975). A heterotrophic epilithic community can resemble that of undisturbed substrates within 13 d (Osborne 1983).

Periphyton begins to regenerate as propagules are transported by the current, perhaps making use of more labile elements of the heterotrophic organic layer. Newly arriving *Baetis* larvae recognize relative abundance of periphyton (Kohler 1984; Richards and Minshall 1988) whose development is tracked by other colonizing grazers (McAuliffe 1983). In an ungrazed community, maximum primary productivity has been attained 21 d after exposure of bare nonstream gravel (Osborne 1983). However, like *Baetis*, not all apparently herbivorous grazers are dependent on periphyton for colonization. Boulton et al. (1988) found that colonization patterns were similar on brushed and acid-scoured stones, although periphyton was slow to develop on the latter. A dominant scraper (*Agapetus*) was found by Lake and Doeg (1985) to be more dense in the colonizing fauna than on surrounding natural stones, perhaps because it is favoured by an early stage in periphyton succession as well as by the relative absence of silt in experimental substrates. Another example of preferential colonization of rocks with depleted periphyton was given by Ogilvie (1988) for the mayfly *Epeorus*, which she called a generalist feeder.

As epilithic growths develop, they change the texture of the substrate surface. Hydropsychid caddisfly larvae require surface irregularities for the attachment of their retreats and capture nets (personal observations). On rough-surfaced rocks, they are early colonizers (personal observations) because, like simuliids, they use seston as food. On smooth rocks, their numbers are small until algal growth or moss is well developed (Hynes 1975; McAuliffe 1983; Dudley et al. 1986). This requirement for rough texture may explain why hydropsychids are later colonizers than simuliids in a Californian stream (Hemphill and Cooper 1983; Hemphill 1988). Hydropsychid retreats, *Rheotanytarsus* tubes, simuliid pupal cocoons (resembling moss), and other structures made by sedentary invertebrates in turn facilitate the colonization of additional taxa by further increasing structural complexity and shelter (Meier et al. 1979; Deutsch 1980; Diamond 1986; Malmqvist and Otto 1987).

3.2.2. Size of substrate particles

Stones in experimental substrate trays do not offer the same range in stone size as natural substrate patches, but do mimic physically disturbed patches in that they are loose, with interstitial spaces at first free of silt and detritus. The size of substrate particle, and hence the size of interstitial spaces, affects colonization in two ways. First, large pebbles and cobbles (>40 mm in diameter) tend to be more stable and, once the surface is suitably conditioned, are more likely than finer substrates to attract clinging sedentary organisms (Khalaf and Tachet 1980; Malmqvist and Otto 1987). The interstitial spaces, however, do not provide as much shelter for small invertebrates as those in gravel, which, if silt free, attract greater densities of organisms than the surrounding substrates (Minshall and Minshall 1977; Williams and Mundie 1978; Shaw and Minshall 1980). Finer experimental substrates tend to collect a different fauna, including more burrowers such as oligochaetes, clams, and chironomine and tanypodine chironomids (Williams and Hynes 1976; Doeg et al. 1989b). A general conclusion from the literature cited is that substrate particle size has conspicuous effects on the density and taxonomic composition of the colonizing fauna.

The second effect of substrate size is on the accumulation and size of detritus particles. Gravel and small pebbles tend to trap more fine particulate organic matter (FPOM) than coarser substrates do, and are colonized by the greatest number of macroinvertebrates (Rabeni and Minshall 1977; Wise and Molles 1979; Parker 1989). In an experiment where fine and medium detritus particles were standardized and evenly distributed among several substrate sizes, Culp et al. (1983) found that invertebrate response to detritus overrode any response to substrate size; but they acknowledged that substrates may be selected by some taxa for attributes other than their detritus-trapping ability. In contrast, Peckarsky (1980) concluded that detritus did not increase colonization by invertebrates, except in summer in a stream where natural leaf inputs were scarce. The introduced detritus in her experiment, however, was in the form of conditioned whole leaves, and may not have attracted gatherers, which are the typical detritivores of the uniform riffle habitats imitated by most experimental substrate trays or cages. Shredders that could have used whole leaves may have been rare in the riffle. Gatherers take advantage of FPOM that rapidly accumulates within the substrates, and are reported to be early (but not always the earliest) colonizers in experiments (Fisher and Gray 1983; Boulton et al. 1988; Parker 1989).

3.3. Competition

As the numbers of browsers, gatherers, filterers, and grazers grow, invertebrates begin to interact with each other. Downes and Lake (1991) have shown that *Austrosimulium torrentium* is a fugitive species, owing its early colonizing success to the absence of other stone-occupying species. Intra- and interspecific competition for space determines the densities of colonizing filterers (Hart 1986; Hemphill 1988; Matczak and Mackay 1990) and grazers (McAuliffe 1983, 1984; Hart 1985). Interactions between individual larvae often lead to density-dependent drift (Hildrew and Townsend 1980; Matczak and Mackay 1990), which is more prevalent among organisms relying on a fixed area of substrate for feeding or other purposes than among more mobile drifters (Ciborowski 1987). Besides causing emigration from the patch under consideration, competition may be occurring upstream, resulting in drift, and hence affecting the rate at which the patch receives immigrants.

3.4. Predation

Predaceous stonefly larvae on substrate patches can reduce colonization by prey taxa (Peckarsky 1985). Significant reductions in total community density as well as changes in the relative numbers of individual taxa were effected by stoneflies moving freely within a substrate cage. The same trend was found when stoneflies were confined in mesh containers and unable to feed, confirming earlier observations on avoidance of predators by prey (Peckarsky and Dodson 1980).

Early colonizers may enjoy an initial period of enemy-free space because dominant predators tend to be later immigrants (e.g. Ulfstrand et al. 1974; Allan 1975; Meier et al. 1979; Shaw and Minshall 1980; Peckarsky 1986; Boothroyd and Dickie 1989). An interesting exception among predators was in a stream where the net-spinning caddisfly *Plectrocnemia conspersa*, which has a high propensity to drift, was an early colonizer (Townsend and Hildrew 1976). Drift of net-spinners is known to result from aggressive interactions over net-spinning space (Hildrew and Townsend 1980; Matczak and Mackay 1990), and serves to distribute larvae among unoccupied habitats. The success of *P. conspersa* as an early immigrant, before a prey community had developed on the patch, could be attributed to the filter-feeding habit; by trapping drifting prey, this predator was independent of prey on the patch itself.

An extreme effect of predation on colonization was seen by Gray and Fisher (1981) in a desert stream, where 117 adult *Deronectes nebulosus* (Dystiscidae) eliminated all mayflies and chironomids in the substrate tray.

4. Timing in Small-Scale Colonization Studies

4.1. Time to Reach Equilibrium

The sequence of events during colonization of bare stream patches has been described in several ways. Classical approaches follow the MacArthur–Wilson island biogeographic model in which community structure progresses towards an equilibrium. It is unlikely that stream communities exist in equilibrium (Lake and Barmuta 1986) although Minshall and Petersen (1985) argued that equilibrial conditions occur under certain flow regimes. Equilibrium is said to be reached on a patch when the arrival rate of new species equals the disappearance rate of other species, and thus the total number of species (strictly, taxa, owing to limitations in identification) becomes more or less constant. Alternative end points in this scheme are the stabilization of either a species diversity index or total densities (or biomass) per patch.

When equilibrium is equated with a plateau in number of species, the apparent colonization period has been as short as 4–6 d in some experiments (Townsend and Hildrew 1976; Lake and Doeg 1985), but more usually is in the range of 10–25 d (Wise and Molles 1979; Lake and Doeg 1985; Minshall and Petersen 1985; Peckarsky 1986). Total invertebrate densities in these experiments seem to have levelled off more slowly in 10–30 d. The times taken for various kinds of introduced substrates to develop equilibrium communities (or stable population densities) were tabulated and discussed by Rosenberg and Resh (1982) who concluded that even when comparisons were limited to rock-filled containers in riffles, colonization times varied according to experimental design, season, and geographic location. Short-term (less than 2 wk) experiments may be unrealistic because an "equilibrium," as defined earlier, cannot develop while substrates are still experiencing changes in epilithic texture and interstitial deposition, which affect the attractiveness and extent of living space. High early departure rates ("extinction") as a result of inhospitability are at odds with the classical model. Some sampling intervals may miss the "colonization" and "extinction" of certain species; and at some seasons, mass immigration or emigration may be occurring in the stream as a whole as a result of egg hatching and emergence.

4.2. Numbers of Individual Taxa

A second method of timing colonization events is to follow changes in numbers of individual taxa. This method shares a problem with the classical one: samples of the "island" fauna usually cannot differentiate between colonists truly exploiting the resources of the patch and individuals that are merely exploring the potentials and moving on. For example, the often recorded early rise in numbers of *Baetis* (e.g. Ulfstrand et al. 1974; Shaw and Minshall 1980; Ciborowski and Clifford 1984; Lake and Doeg 1985; Dudley 1988) probably includes much coming and going while larvae test periphyton resources before eventually staying longer to feed. On the other hand, the equally sharp rise in Simuliidae (e.g. Ulfstrand et al. 1974; Lake and Doeg 1985) is more likely to reflect true colonization of bare sites for filter feeding. A later decline in simuliid densities has been explained as part of the colonization sequence as larvae avoid growing densities of algae and other filter feeders (Lake and Doeg 1985; Hemphill 1988; Downes and Lake 1991) or simply as due to emergence (Khalaf and Tachet 1977).

In spite of uncertainties as to true colonization versus exploration, the individual-species approach reveals which types of organisms are available and able to take advantage of changing resources. Using this approach, colonization may be described as complete either when number of individuals per taxon becomes stable or when final densities and relative proportions of the various taxa match those in the community surrounding the patch being studied. If colonization is being used as a measure of recovery, then comparing assemblages on experimental substrates with those surrounding them is the better guide. Rather few small-scale studies have done this in a systematic way. Short-term experiments have found inconsistencies in the comparisons when early colonizers were overrepresented by drifters from upstream habitats (Ciborowski and Clifford 1984). Longer studies (e.g. Boothroyd and Dickie 1989; Doeg et al. 1989a) allow time for immigration by less mobile species and show how certain unexpected changes in experimental patch densities may be explained by similar changes in natural substrates. Lake and Doeg's (1985) comparison of different equilibrium criteria in the Acheron and Toorongo rivers showed that the numbers of colonizing species over time levelled off conspicuously over 8 d but took 16 or 32 d, respectively, to reach the numbers found in the surrounding riffles.

4.3. Effects of Season and Life History

Timing of events is heavily dependent on season. In yearlong or multiseasonal studies, colonization has been reported as being faster in summer and early fall in perennial temperate streams (Shaw and Minshall 1980; Williams 1980; Doeg et al. 1989a). In most temperate streams, recruitment in general is higher at these seasons for many species. Dispersal (drift, crawling) from crowded egg-hatching sites, oviposition directly on experimental substrates, and greater activity at higher temperatures all increase chances of invertebrates being recovered on the newly available introduced space. Faster periphyton development in summer increases the rate at which epilithic growths attract and sustain grazers. In Australia, where summer is the season of peak riparian litter fall (Bunn 1986; Lake et al. 1986), benthic organic matter accumulated faster in experimental patches in summer than in winter (Doeg et al. 1989a) and may have attracted colonizers. The more colonizing mechanisms that are available at any one time, the faster colonization will be at that time.

The effect of invertebrate life history on colonization is more complex than the simple seasonal recruitment mentioned above. If colonizing propagules for a species are limited to a particular life history stage, e.g. gravid females ovipositing directly, or age-restricted drifters, then at times when propagules are unavailable, fewer colonizers can be expected on experimental substrates even though the species is present in the surrounding benthos. This limitation might explain why substrates in Lake and Doeg's (1985) Acheron II experiment, which was carried out in winter, never matched natural substrates in number of species and why chironomids, which were known to be mainly summer drifters, were slow to colonize substrates in another winter experiment in the Acheron River (Doeg et al. 1989a). When propagules are produced more frequently or are active over longer periods, colonization is completed more quickly. For example, rapid colonization in intermittent desert streams has been attributed to nearly year-round oviposition by some insects owing to long-lived females or to wide-ranging flight from asynchronous populations in permanent habitats (Gray 1981). Asynchrony and the lack of seasonality in life cycles of many New Zealand stream-living insects mean that emergence and oviposition can take place over many months (Winterbourn 1978; Towns 1981). Australian populations also seem to be poorly synchronized (Marchant 1986). Insects are not the only invertebrates with asynchronous development. *Gammarus*, too, is often seen in a wide range of size classes so that appropriate sizes for scavenging among bare patches are always available, as well as reproductive stages (Ulfstrand et al. 1974).

5. Small-Scale Studies of Disturbance Intensity and Frequency

The basic supposition, when introducing experimental substrates into streams, is that the particular treatment mimics some level of natural disturbance. Thus, rocks that are picked clean of invertebrates, but not dried or scraped, are equivalent to stream substrates subjected to some tumbling or shifting, which washes away associated animals and interstitial silt but leaves rock texture intact, together with attached microbial and algal growths. Scrubbing and drying remove live epilithon, but may leave some regenerating material. Disturbances severe enough to scour away basal epilithic structures and marl have been simulated by substituting quarry stones, or by exposing natural stream rocks to acid or mechanical abrasion.

During a month-long colonization experiment, Lake and Doeg (1985) found considerably fewer species on quarry stones than on previously brushed and dried river stones, except on the final day. Invertebrate density on quarry stones levelled off after 15 d whereas density on river stones continued to rise, with conspicuously higher numbers of scraper-grazers. Even brushed and dried river stones were quickly able to generate a sustaining epilithon for scrapers. In a similar comparison, Bolton et al. (1988) scoured stones from another Australian river in 2 N nitric acid to mimic severe disturbance. Epilithon recovery, as expected, was slow, and scraper densities were far lower than those on control rocks. However, *Baetis* densities rose rapidly to match control rocks within 8 d, and colonization curves for several other taxa and total densities, although somewhat lower, were similar in shape to control curves despite poor epilithic development. These comparative experiments demonstrated consistent patterns of colonization, with the same sequence of early and late taxa even though densities were different.

The frequency as well as the intensity of disturbance has been tested in small-scale experiments. In a Rocky Mountain stream, bricks that were turned over at frequent intervals supported less periphyton and had lower invertebrate species richness and density than bricks turned less often (Robinson and Minshall 1986). This kind of high-elevation mountain stream normally experiences a predictable major rise in discharge only at snowmelt, which is so predictable that Resh et al. (1988) did not consider it to be a real disturbance. Rather, it is a seasonal event to which organisms are adapted in terms of life history and behaviour. In such a stream, spates at other seasons are indeed disturbances; and the more frequent the occurrence, the more severe the impact, as shown by experimental overturning of rocks at these seasons (Robinson and Minshall 1986).

In contrast, colonization experiments in streams exposed to irregular spates throughout the year do not show clear correlations between disturbance frequency and community recovery. In a southeastern USA stream, Reice (1984, 1985) showed that recovery of riffle invertebrates after experimental rock tumbling was the same in terms of species richness and diversity whether tumbling had occurred only once or twice (after a 2-wk interval). Stream substrates raked three times over 20 d in the Acheron River recovered as quickly as patches raked only once (Lake et al. 1989). In this Australian river, individual species were also unaffected by disturbance frequency, suggesting that all taxa were well able to cope with repeated disruptions of the streambed.

6. Disturbance and Colonization on a Larger Scale

The small-scale studies reviewed so far are reasonable simulations of the colonizing events that might follow local disruptions and minor spates. Natural rocks surrounding an experimentally denuded patch are like sheltered bays and the hyporheic zone following moderate increases in discharge: both harbour potential colonizers. The proximity of so many colonizers, however, means that colonization rates are probably far higher in small-scale experiments than in situations when more of the streambed is affected. Manipulative experiments on whole streams are understandably rare, but studies of new channels and of streams recovering from drought, extreme spates or floods, and certain types of pollution have all provided information on colonization or recovery rates.

6.1. Disturbed Reaches

Where disruption is severe but local, as in the case of polluting inputs, the substrate is occupied by stream invertebrates as soon as it is able to provide shelter and food. For example, in a stream polluted by a gasoline spill, invertebrates recovered from a 2–25% reduction in densities within 7 mo (with reference to an upstream site) and reached full species richness within 16 mo (Pontasch and Brusven 1988). The sequential downstream recovery of study sites, as well as the lag in restoration of species richness, suggested that drift was the most important colonizing mechanism. Normal drift by organisms immediately upstream was probably occurring during the severely polluted period, but settling was not permanent until the habitat became hospitable. Habitat recovery was aided partly by mechanical agitation 1 mo after the spill to remove hydrocarbons, and partly by dense periphyton blooms (Pontasch and Brusven 1987) which provided abundant food not only for grazers but also, perhaps, for gatherers as sestonic FPOM was trapped and the algae later decayed. In contrast, a stream relocated along a uniformly wide, flat-bottomed channel filled with gravel and silty sand provided neither interstitial habitats for riffle macroinvertebrates nor suitable structures for periphyton development and leaf-pack accumulations (Narf 1985). Instead, silt flushed out of the new channel was a pollutant. Not until 5 yr later, when cobbles had been washed free of silt, did the colonizing fauna match the upstream reference site. A similar pollutant, volcanic ash from the 1980 eruption of Mt. St. Helens, was blamed for the slow (>5 yr) recovery of the caddisfly fauna in streams within the blast zone (Anderson and Wisseman 1987).

Another example of recovery after severe local disturbance was given by Lamberti et al. (1991) who described the effect of a catastrophic debris flow on a forested stream. Vagile herbivores like chironomids and baetids matched upstream densities within 1 yr, and less mobile herbivores (glossosomatids and pleurocerid snails) did so within 2 yr. Shredders and predators were late colonizers. Rapid recoveries were attributed to increased primary production in the disturbed reach, which provided food-rich habitat for colonizers arriving by drift and oviposition.

6.2. New Channels and Recovery from Drought and Washouts

Examples of colonization on a truly large scale were provided by a newly opened 0.6-km channel that rerouted the Tongue River, Wyoming, across nonriverine substrates (Gore 1979, 1982) and by the rewatering of the North Fork of the Teton River, Idaho, after exposure first to catastrophic discharge, and then to 3.5 mo (August–December) without flow following deliberate diversion upstream (Minshall et al. 1983).

In both cases, the river upstream from the new or dewatered channel was clearly the chief source of colonizers because the rate at which sequential study sites were colonized was directly related to distance from this source. The colonization site near the lower end of the Tongue River new channel received later immigrants from the recognizable established community in the river downstream, presumably by upstream crawling. Aerial colonization was also possible during at least the first 3 wk of the study (August). In the Teton River, the distance (>20 km) of the study sites from the Snake River downstream, and the December opening of the North Fork, meant that drift was probably the only colonizing mechanism there for the first few months; dewatering had destroyed resident populations, at least within the top 50 cm of streambed. During the first 5 mo of the Tongue River rerouting, the station closest to the source of colonizers approached equilibrium more rapidly than the two more distant stations, which were similarly staggered. This was true whether equilibrium was measured in terms of invertebrate densities, number of taxa, or a community structure resembling the upstream source of colonizers. A similar sequence was seen in the Teton River. Both sets of data were in accordance with the predictions of the island biogeographic theory of colonization from a single ''mainland'' source, although Gore (1982) recognized that the strict MacArthur–Wilson model, with its continued isolation of islands, would no longer apply once the new channel became continuous with the source area in substrate texture and food.

The time taken to reach ''equilibrium'' in the Tongue and Teton rivers depended on the way equilibrium was defined and measured. In the Tongue River new channel, densities and community similarity comparable with the river upstream were reached within 70 and 125 d, respectively, but species richness did not become constant until ~300 d after the new channel was opened (Gore 1979, 1982). In the Teton River, total numbers recovered in ~375 d and cumulative species richness in ~700 d (Minshall et al. 1983). In both rivers, the number of taxa per collection (species richness) lagged behind number of individuals. This lag contrasts with small-scale studies where numbers of taxa tended to level off early; it may be explained by the importance of drift in the newly watered channels and the fact that certain species are far more prevalent than others in the drift. If other colonizing sources had been available, then more species might have been represented sooner. Indeed, in the Tongue River new channel, where upstream movement and aerial colonization were possible from nearby sources (<1 km away), the lag was not as pronounced as in the Teton River.

Some clear trends are obvious in the Tongue and the Teton studies which confirm patterns seen during small-scale experiments. In the Tongue River new channel, early colonizers were *Baetis* species, simuliid (first) and hydropsychid (second) filter feeders, and chironomids (Gore 1979), which Gore (1982) categorized as collector-gatherers and collector-filterers. Scrapers arrived a few days later. Minshall et al. (1983) provided few data on individual taxa in the Teton, but noted that *Baetis* and chironomids colonized within days of rewatering. *Baetis*, at least, seems to have been termed a grazer in the Teton River, for grazers were generally predominant during the early stages of recolonization, but were soon replaced by collectors (presumably including gatherers as well as filterers). In both rivers, predators and shredders were late arrivals and low in abundance.

The Tongue and Teton River studies of newly watered channels dealt only with true colonization because the existence of resistant stages in the dry channel was virtually impossible in the Tongue River and unlikely in the Teton. When drought occurs regularly, perhaps on a seasonal or annual basis, returning water revives survivors as well as attracting colonizers from elsewhere. Some survivors (e.g. certain species of mayflies, chironomids, and simuliids) hatch from drought-resistant eggs (Hynes 1958; Williams 1977). Others venture from refuges in the hyporheos, damp spots under rocks and organic debris, and isolated stream pools (Clifford 1966; Hynes 1975; Boulton 1989).

Where streams are too sunbaked to allow survival in the streambed, as in some African streams during drought (Harrison 1966; Hynes 1975), colonization is most likely from eggs laid by aerial adults when flow resumes, followed by rapid hatching and growth. Mature baetid (*Centroptilum*) nymphs and chironomid pupae developed within 18 d in a tributary to the Pawmpawm River in Ghana (Hynes 1975). In the Pawmpawm River itself, the first colonizers included simuliids as well as baetid and chironomid gatherers; baetid and hydropsychid predators were later.

Even streams recovering from catastrophic washouts may be recolonized by survivors, these being either exceptionally deeply buried — such as tabanid larvae in a desert stream (Gray 1981) — or sheltered in debris on the edge of floodwaters from which they return as floods recede (Cushing and Gaines 1989). More often, recovery is through oviposition by aerial insects (Siegfried and Knight 1977; Gray and Fisher 1981) that either emerged from the stream before disturbance and were long lived (Gray 1981) or immigrated after emergence from neighbouring streams (Resh 1982). Colonization rates obviously will be faster if the disturbance occurs at a time when insects are most likely to be on the wing. The recovery of Burns Run, a normally stable stream in Pennsylvania, after Hurricane Agnes caused a 150-fold increase in discharge (Hoopes 1974), probably owed much to the early date (June) of the storm, which meant oviposition was possible over the rest of the summer. Summer, however, is not always a favourable season. Contrasting effects of winter spates (regular events to which the fauna was assumed to be adapted) and an unexpected and severe spate in summer were described by Giller et al. (1991) for an Irish stream. In this tributary of the River Araglin, recovery was relatively rapid after the winter spates, but was much slower (>3 yr) after the summer spate.

6.3. Unstable Rivers

Rivers that experience frequent fluctuations in discharge, much bed movement, and high loads of suspended sediment inflict the most difficult conditions on their benthic faunas, and consequently provide interesting information on tolerance and resilience. Recent studies of such large unstable rivers in New Zealand (Sagar 1986; Scrimgeour et al. 1988; Scrimgeour and Winterbourn 1989) showed that although invertebrate densities are severely reduced after major spates, mainly through abrasion of algal food as well as direct damage, certain taxa are able to recover quickly. These taxa are mostly collector-browsers, such as the leptophlebiid mayfly *Deleatidium* and chironomid larvae, filter-feeding hydropsychids (*Aoteapsyche*), and predatory hydrobiosid caddisflies. Larvae avoid spates to some extent by burrowing into the substrate (even normally sedentary hydropsychids do this: Poole and Stewart 1976; R. J. Mackay, unpublished data) or by surviving in sheltered segments of these braided rivers (Scrimgeour et al. 1988; Scrimgeour and Winterbourn 1989). Denuded braids are recolonized either by drift (Sagar 1983) or by ovipositing adults coming from refuge braids (Scrimgeour et al. 1988). Most of these colonizing species are present in a wide range of size classes throughout the year, and thus have the potential to mature and multiply rapidly during stable flow regimes.

In unstable New Zealand rivers, *Deleatidium* species seem to be particularly resilient. Part of their success may result from their habit of browsing the rapidly regenerating organic layers on stones, which are important food materials in New Zealand rivers (Rounick and Winterbourn 1983; Collier and Winterbourn 1990). In the Inangahua River, New Zealand, bed materials are continually being abraded by fine sediments, and algal growths are unable to become well established. Even though other invertebrates apparently feed on fragments of allochthonous materials that are alternately mobilized in spates and trapped in depositional sites, Winterbourn et al. (1984) found that *Deleatidium* probably derives much of its carbon from dissolved organic material taken up by the epilithic microbial layer.

After reviewing the literature on spatial and temporal heterogeneity in streambeds, Poff and Ward (1990) concluded that streams with a greater historical record of such heterogeneity will express greater persistence, resistance, and rate of recovery than less variable systems, largely because the biota is adapted to cope with the conditions.

7. Colonization Patterns

7.1. Taxa and Trophic Groups of Primary Consumers

When colonizers of experimental patches, disturbed reaches, newly watered channels, and disturbed rivers are compared around the world, taxa recur with remarkable concordance at the family level and are often identical (or close relatives) at the generic level. Among the mayflies, Baetidae (mostly *Baetis*) are abundant and early colonizers in most parts of the world (e.g. Ulfstrand et al. 1974; Hynes 1975; Gore 1979; Gray and Fisher 1981; Minshall et al. 1983; Lake and Doeg 1985; Boulton et al. 1988; Parker 1989; Lamberti et al. 1991). Certain Leptophlebiidae are similarly recorded, such as *Deleatidium* in New Zealand (Sagar 1986; Scrimgeour et al. 1988) and *Atalonella* and *Atalophlebiodes* in Australia (Lake and Doeg 1985; Boulton et al. 1988). *Baetis* may share the browsing habit of *Delatidium* if it is capable of removing thin organic films. The other leptophlebiids could be browsers too, or they may be gatherers as they are in North America (Lamberti and Moore 1984; Merritt and Cummins 1984). Chironomidae are consistently recorded among the first colonizers (most studies of new or disturbed substrates), especially after scouring spates and washouts (McElravy et al. 1989). When chironomids have been identified beyond family (e.g. Gray and Fisher 1981; Sagar 1986; Doeg et al. 1989a; Parker 1989), orthocladiine gatherers are predominant. The early arrival of all the above browsers and gatherers is consistent with their ability to exploit the earliest food materials on and among bare substrates. Fisher et al. (1982) found that gatherers composed 87% of numbers and 85% of biomass in the invertebrate community of a desert stream disturbed by flash floods. Later in the recovery of streams, a grazing habit may be adopted by browsers, and additional herbivorous taxa contribute to colonization.

If colonists cannot browse or gather, the alternative early feeding strategy is filtering, making use of suspended fine detritus which is nearly always present in disturbed streams. Simuliidae, Hydropsychidae, and some chironomine chironomids (*Rheotanytarsus*) are reported repeatedly. Because the hydropsychids can only establish retreats on rough-surfaced rocks, they are not always the earliest filterers. Nevertheless, they have some characteristics of opportunists in that the genera most often reported (*Aoteapsyche*, *Asmicridea*, *Cheumatopsyche*, *Hydropsyche*, and *Symphitopsyche*) are in the subfamily Hydropsychinae. Larvae in this subfamily tend to have unspecialized nets and a broad diet (Fuller and Mackay 1980), and they can feed on drifting animals as well as detrital seston (Lamberti and Moore 1984).

Shredder-dominated communities, such as those in first-order forested streams, are rather slow to recover after disturbance (Wallace 1990), and shredders have often been reported as later colonizers than other detritivores and herbivores (Gray and Fisher 1981; Gore 1982; Minshall et al. 1983; Boulton et al. 1988; Doeg et al. 1989a; Lamberti et al. 1991). Many shredders have poor dispersal abilities (Wallace et al. 1986). With the exception of *Gammarus*, shredders are rather rare in the drift (Waters 1972), so they are not routinely transported to disturbed reaches from upstream sources. Coarse particulate organic matter (CPOM) concentrations tend to be more seasonal than FPOM, and may not be immediately supplied to a disturbed patch or stream. Shredder life cycles tend to be long (Wallace et al. 1986) and tied to seasonal inputs and decay of CPOM. Many life cycles are synchronous. Therefore, colonizing stages may not be available following an unexpected disturbance. The relatively few numbers of shredders among early colonizers of introduced substrates could be the result of a low shredder density in the study riffle (a possible explanation for Peckarsky's (1980) results) and the slow rate of CPOM accumulation. When CPOM did collect on substrate trays in a suitable stream, many shredders were among the colonizers (Ulfstrand et al. 1974).

7.2. Mobility and Life Cycles

The recurring taxa include many of those that were described earlier as drifters, swimmers, and rapid crawlers. Some adult insects are strong fliers, like the beetles that may be conspicuous in streams recovering from drought. Some adults are short-lived; but asynchronous life cycles, as seen in Australian and New Zealand streams, mean that propagules could be available for colonization at all times, especially if headwaters, side channels, or nearby streams provide refuges from which propagules can disperse to restored habitats. In fluctuating environments, successful colonizers have life cycles that allow them to take advantage of temporary benign periods in disturbed streams, and at the same time to benefit from such features in these streams as unsilted substrates and early successional stages in periphyton development.

Temperatures supporting maximum growth rates will obviously provide the fastest regeneration of populations. Usually these are warm temperatures (annual mean >15°C) which, in the southern USA at least, allow development times as short as 6–15 d for chironomids (Gray 1981; Stites and Benke 1989), 9 d for black flies (Hauer and Benke 1987), and 10–19 d for *Baetis* (Gray 1981; Benke and Jacobi 1986). However, Hauer and Benke (1991) found that high growth rates recorded for chironomids in the Ogeechee River were related not only to temperature but also to high discharge (>20 m^3/s). They attributed the growth response to the higher seston concentration associated with high discharge. High growth rates in cool-adapted species, too, allow them to be pioneers in new or disturbed streams. One of these species is *Orthocladius calvus*, with a development time in southern England (52°N) of 16 d. This species not only colonized a new gravel channel with remarkable rapidity, but was so specialized for this kind of virgin habitat that it was not known from typical stream communities in the area (Ladle et al. 1985).

7.3. General Predictions

Benthic communities will develop and stabilize sooner if the disturbance that originally denuded the substrate is a local rather than a regionally extensive catastrophe. If upstream reaches, side channels, and neighbouring drainages are unaffected, the surviving benthos and ovipositing adults soon provide colonizers. Recovery will be faster if the colonization period coincides with reproductive periods in the benthos. Colonization by shredders that are closely tied to allochthonous organic inputs could be restricted by season. Likewise, certain algal scrapers have a limited period of activity dependent on the productivity of epilithic algae. Such seasonally bound life cycles in streams that normally experience only regular climatic events could limit colonization when the biota is damaged by an unexpected disturbance.

Streams most likely to recover quickly are runoff streams, in which discharge is often irregular and unpredictable (Poff and Ward 1990). They include perennial and intermittent upland streams in Victoria (Lake et al. 1985, 1988) and agricultural Ontario (Mackay 1979) as well as the more flashy flows typical of New Zealand (Winterbourn et al. 1981), coastal California (McElravy et al. 1989), and deserts (Fisher et al. 1982). Many of these streams are in a climate that allows long periods of oviposition, asynchronous life cycles, and high growth rates, all of which favour the availability of propagules and the rapid exploitation of newly available or restored habitats.

Recurring ecological patterns are seen in the repopulating species. Many of the same taxa and functional groups are involved. Lotic invertebrate communities likely to be resilient after disturbance will include substantial proportions of baetid, leptophlebiid, and sometimes heptageniid mayflies, multivoltine black flies, especially fugitive species, opportunistic orthocladine browsers and gatherers, clinging chironomine filterers like *Rheotanytarsus*, and Hydropsychine caddisflies. Where periphytic algae regenerate quickly, grazers will colonize soon after detritivores.

In the nonequilibrium conditions of disturbed streams, communities are thought to be controlled in a stochastic manner (Wallace 1990). However, although a disturbance may indeed occur by chance, the same cannot be said of the ability of the disturbed community to ''bounce back.'' There is some degree of predictability if the fauna is known. Depending on hydrologic regime and season, predictions can be made on the likely responses of lotic invertebrates to disturbance, according to their ecological traits and dynamics. The ability of a stream to cope with disturbance could be assessed. This kind of information could be invaluable to planners debating the necessity of protecting a stream. For although our ecological knowledge at the species level is still incomplete, some recognition of typical faunal patterns can provide the constructive advice needed in environmental decision-making.

Acknowledgements

Helpful comments were received from Bobbi Peckarsky, Sam Lake, Seth Reice, and Colin Levings, which improved the focus and organization of this review. Preparation of the paper was aided by an operating grant from the Natural Sciences and Engineering Research Council of Canada, for which I am grateful.

References

Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology 56: 1040–1053.

Anderson, N. H., and R. W. Wisseman. 1987. Recovery of the Trichoptera fauna near Mt. St. Helens five years after the 1980 eruption, p. 367–373. *In* M. Bournaud and H. Tachet [ed.] Proc. of the 5th Int. Symp. on Trichoptera. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Beckett, D. C., and M. C. Miller. 1982. Macroinvertebrate colonization of multiplate samplers in the Ohio River: the effect of dams. Can. J. Fish. Aquat. Sci. 39: 1622–1627.

Benke, A. C., and D. J. Jacobi. 1986. Growth rates of mayflies in a subtropical river and their implications for secondary production. J. N. Am. Benthol. Soc. 5: 107–114.

Benson, L. J., and R. G. Pearson. 1987. Drift and upstream movement in Yuccabine Creek, an Australian tropical stream. Hydrobiologia 153: 225–239.

Benzie, J. A. H. 1984. The colonization mechanisms of stream benthos in a tropical river (Menik Ganga: Sri Lanka). Hydrobiologia 111: 171–179.

Bird, G. A., and H. B. N. Hynes. 1981. Movement of immature aquatic insects in a lotic habitat. Hydrobiologia 77: 103–112.

Boothroyd, I. K. G., and B. N. Dickie. 1989. Macroinvertebrate colonisation of perspex artificial substrates for use in biomonitoring studies. N.Z. J. Mar. Freshwater Res. 23: 467–478.

Boulton, A. J. 1989. Oversummering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. Trans. R. Soc. S. Aust. 113: 23–34.

Boulton, A. J., G. M. Spangaro, and P. S. Lake. 1988. Macroinvertebrate distribution and recolonization on stones subjected to varying degrees of disturbance — an experimental approach. Arch. Hydrobiol. 113: 551–576.

Bunn, S. E. 1986. Origin and fate of organic matter in Australian upland streams, p. 277–291. *In* P. deDecker and W. D. Williams [ed.] Limnology in Australia. Monogr. Biol. Vol. 61. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Calow, P. 1975. On the nature and possible utility of epilithic detritus. Hydrobiologia 46: 181–189.

Chutter, F. M. 1968. On the ecology of the fauna of stones in the current in a South African river supporting a very large Simulium population. J. Appl. Ecol. 5: 531–561.

Ciborowski, J. J. H. 1987. Dynamics of drift and microdistribution of two mayfly populations. Can. J. Fish. Aquat. Sci. 44: 832–845.

Ciborowski, J. J. H., and H. F. Clifford. 1984. Short-term colonization patterns of lotic macroinvertebrates. Can. J. Fish. Aquat. Sci. 41: 1626–1633.

Ciborowski, J. J. H., and L. D. Corkum. 1980. Importance of behaviour to the re-establishment of drifting Ephemeroptera, p. 321–330. *In* J. F. Flannagan and K. E. Marshall [ed.] Advances in Ephemeroptera biology. Plenum Press, New York, NY.

Clifford, H. F. 1966. The ecology of invertebrates in an intermittent stream. Invest. Indiana Lakes Streams 7: 57–98.

Collier, K. J., and M. J. Winterbourn. 1990. Population dynamics and feeding of mayfly larvae in some acid and alkaline New Zealand streams. Freshwater Biol. 23: 181–189.

Culp, J. M., S. J. Walde, and R. W. Davies. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. Can. J. Fish. Aquat. Sci. 40: 1568–1574.

Cushing, C. E., and W. L. Gaines. 1989. Thoughts on recolonization of endorheic cold desert spring-streams. J. N. Am. Benthol. Soc. 8: 277–287.

Deutsch, W. G. 1980. Macroinvertebrate colonization of acrylic plates in a large river. Hydrobiologia 75: 65–72.

1984. Oviposition of Hydropsychidae (Trichoptera) in a large river. Can. J. Zool. 62: 1988–1994.

Diamond, J. M. 1986. Effects of larval retreats of the caddisfly *Cheumatopsyche* on macroinvertebrate colonization in Piedmont, USA streams. Oikos 47: 13–18.

Doeg, T. J., P. S. Lake, and R. Marchant. 1989a. Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. Aust. J. Ecol. 14: 207–220.

Doeg, T. J., R. Marchant, M. Douglas, and P. S. Lake. 1989b. Experimental colonization of sand, gravel and stones by macroinvertebrates in the Acheron River, southeastern Australia. Freshwater Biol. 22: 57–64.

Downes, B. J., and P. S. Lake. 1991. Different colonization patterns of two closely related stream insects (*Austrosimulium* spp.) following disturbance. Freshwater Biol. 26: 295–306.

Dudley, T. L. 1988. The roles of plant complexity and epiphyton in colonization of macrophytes by stream insects. Verh. Int. Ver. Limnol. 23: 1153–1158.

Dudley, T. L., S. D. Cooper, and N. Hemphill. 1986. Effects of macroalgae on a stream invertebrate community. J. N. Am. Benthol. Soc. 5: 93–106.

Fisher, S. G., and L. J. Gray. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. Ecology 64: 1217–1224.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecol. Monogr. 52: 93–110.

Fuller, R. L., and R. J. Mackay. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Can. J. Zool. 58: 2239–2251.

Geesey, G. G., R. Mutch, J. W. Costerton, and R. B. Green. 1978. Sessile bacteria: an important component of the microbial population in small mountain streams. Limnol. Oceanogr. 23: 1214–1223.

Gersabeck, E. F., and R. W. Merritt. 1979. The effect of physical factors on the colonization and relocation behavior of immature black flies (Diptera: Simuliidae). Environ. Entomol. 8: 34–39.

Giller, P. S., and R. N. B. Cambell. 1989. Colonization patterns of mayfly nymphs (Ephemeroptera) on implanted substrate trays of different size. Hydrobiologia 178: 59–71.

Giller, P. S., N. Sangpradub, and H. Twomey. 1991. Catastrophic flooding and macroinvertebrate community structure. Verh. Int. Ver. Limnol. 24: 1724–1729.

Gore, J. A. 1979. Patterns of initial benthic recolonization of a reclaimed coal strip-mined river channel. Can. J. Zool. 57: 2429–2439.

1982. Benthic invertebrate colonization: source distance effects on community composition. Hydrobiologia 94: 183–193.

Gore, J. A., and A. M. Milner. 1990. Island biogeographical theory: can it be used to predict lotic recovery rates? Environ. Manage. 14: 737–753.

Gray, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoron Desert stream. Am. Midl. Nat. 106: 229–242.

Gray, L. J., and S. G. Fisher. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. Am. Midl. Nat. 106: 249–257.

Harrison, A. D. 1966. Recolonisation of a Rhodesian stream after drought. Arch. Hydrobiol. 62: 405–421.

Hart, D. D. 1981. Foraging and resource patchiness — field experiments with a grazing stream insect. Oikos 37: 46–52.

1985. Causes and consequences of territoriality in a grazing stream insect. Ecology 66: 404–414.

1986. The adaptive significance of territoriality in filter-feeding larval black flies (Diptera: Simuliidae). Oikos 46: 88–92.

Hart, D. D., and V. H. Resh. 1980. Movement patterns and foraging ecology of a stream caddisfly larva. Can. J. Zool. 58: 1174–1185.

Hauer, F. R., and A. C. Benke. 1987. Influence of temperature and river hydrograph on black fly growth rates in a subtropical blackwater river. J. N. Am. Benthol. Soc. 6: 251–261.

1991. Rapid growth of snag-dwelling chironomids in a blackwater river: the influence of temperature and discharge. J. N. Am. Benthol. Soc. 10: 154–164.

Hayden, W., and H. F. Clifford. 1974. Seasonal movements of the mayfly *Leptophlebia cupida* (Say) in a brown-water stream of Alberta, Canada. Am. Midl. Nat. 91: 90–102.

Hemphill, N. 1988. Competition between two stream dwelling filter feeders, *Hydropsyche oslari* and *Simulium virgatum*. Oecologia 77: 73–80.

Hemphill, N., and S. D. Cooper. 1983. The effect of physical disturbance on the relative abundance of two filter-feeding insects in a small stream. Oecologia 58: 378–382.

Hershey, A. E., and A. L. Hiltner. 1988. Effect of a caddisfly on black fly density: interspecific interactions limit black flies in an arctic river. J. N. Am. Benthol. Soc. 7: 188–196.

Hildrew, A. G., and C. R. Townsend. 1980. Aggregation, interference and foraging by larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropodidae). Anim. Behav. 28: 553–560.

Hoopes, R. L. 1974. Flooding, as the result of Hurricane Agnes, and its effect on a macrobenthic community in an infertile headwater stream in central Pennsylvania. Limnol. Oceanogr. 19: 853–857.

Hynes, H. B. N. 1958. The effect of drought on the fauna of a small mountain stream in Wales. Verh. Int. Ver. Limnol. 13: 826–833.

1970. The ecology of running waters. University of Toronto Press, Toronto, Ont. 555 p.

Hynes, J. D. 1975. Annual cycles of macro-invertebrates of a river in southern Ghana. Freshwater Biol. 5: 71–83.

Imhof, J. E., and S. M. Smith. 1979. Oviposition behaviour, egg-masses and hatching response of the eggs of five Nearctic species of *Simulium* (Diptera: Simuliidae). Bull. Entomol. Res. 69: 405–425.

Khalaf, G., and H. Tachet. 1977. La dynamique de colonisation des sustrats artificiels par les macroinvertébrés d'un cours d'eau. Ann. Limnol. 13: 169–190.

1980. Colonization of artificial substrata by macro-invertebrates in a stream and variations according to stone size. Freshwater Biol. 10: 475–482.

Kohler, S. L. 1984. Search mechanism of a stream grazer in patchy environments — the role of food abundance. Oecologia 62: 209–218.

1985. Identification of stream drift mechanisms: an experimental and observational approach. Ecology 66: 1749–1761.

Kohler, S. L., and M. A. McPeek. 1989. Predation risk and the foraging behaviour of competing stream insects. Ecology 70: 1811–1825.

Ladle, M., D. A. Cooling, J. S. Welton, and J. A. B. Bass. 1985. Studies on Chironomidae in experimental recirculating stream systems. II. The growth, development and production of a spring generation of *Orthocladius* (*Euorthocladius*) *calvus* Pinder. Freshwater Biol. 15: 243–255.

Lake, P. S., and L. A. Barmuta. 1986. Stream benthic communities: persistent presumptions and current speculations, p. 263–276. *In* P. deDecker and W. D. Williams [ed.] Limnology in Australia. Monogr. Biol. Vol. 61. Dr. W. Junk Publishers Dordrecht, The Netherlands.

Lake, P. S., L. A. Barmuta, A. J. Boulton, I. C. Campbell, and R. M. St. Clair. 1986. Australian streams and Northern Hemisphere stream ecology: comparisons and problems. Proc. Ecol. Soc. Aust. 14: 61–82.

Lake, P. S., and T. J. Doeg. 1985. Macroinvertebrate colonization of stones in two upland southern Australian streams. Hydrobiologia 126: 199–212.

Lake, P. S., T. J. Doeg, and R. Marchant. 1989. Effects of multiple disturbance on macroinvertebrate communities in the Acheron River, Victoria. Aust. J. Ecol. 14: 507–514.

Lake, P. S., T. J. Doeg, and D. W. Morton. 1985. The macroinvertebrate community of stones in an Australian upland stream. Verh. Int. Ver. Limnol. 22: 2141–2147.

Lake, P. S., D. W. Morton, and B. J. Milne. 1988. Interspecific associations in the faunal assemblages of stones of an Australian upland stream. Verh. Int. Ver. Limnol. 23: 1384–1387.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and K. M. S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. Can. J. Fish. Aquat. Sci. 48: 196–208.

Lamberti, G. A., and J. W. Moore. 1984. Aquatic insects as primary consumers, p. 164–195. *In* V. H. Resh and D. M. Rosenberg [ed.] The ecology of aquatic insects. Praeger Publishers, New York, NY.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ. 203 p.

Mackay, R. J. 1979. Life history patterns of some species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Can. J. Zool. 57: 963–975.

Madsen, B. L. 1972. Detritus on stones in small streams. Mem. Ist. Ital. Idrobiol. 29(Suppl.): 385–403.

Malmqvist, B., and C. Otto. 1987. The influence of substrate stability on the composition of stream benthos — an experimental study. Oikos 48: 33–38.

Marchant, R. 1986. Some quantitative aspects of the life history of aquatic insects in temperate Australian rivers, p. 151–158. *In* P. deDecker and W. D. Williams [ed.] Limnology in Australia. Monogr. Biol. Vol. 61. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Matczak, T. Z., and R. J. Mackay. 1990. Territoriality in filter-feeding caddisfly larvae: laboratory experiments. J. N. Am. Benthol. Soc. 9: 26–34.

May, R. M. 1984. An overview: real and apparent patterns in community structure, p. 3–16. *In* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle [ed.] Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, NJ.

McAuliffe, J. R. 1983. Competition, colonization patterns, and disturbance in stream benthic communities, p. 137–155. *In* J. R. Barnes and G. W. Minshall [ed.] Stream ecology: application and testing of general ecological theory. Plenum, New York, NY.

1984. Competition for space, disturbance, and the structure of a benthic stream community. Ecology 65: 894–908.

McElravy, E. P., G. A. Lamberti, and V. H. Resh. 1989. Year to year variation in the aquatic macroinvertebrate fauna of a northern California stream. J. N. Am. Benthol. Soc. 8: 51–63.

Meier, P. G., D. L. Penrose, and L. Polak. 1979. The rate of colonization by macroinvertebrates on artificial substrate samplers. Freshwater Biol. 9: 381–392.

Merritt, R. W., and K. W. Cummins [ed.] 1984. An introduction to the aquatic insects of North America. 2nd ed. Kendall/Hunt Publishing Company, Dubuque, IA. 722 p.

Minshall, G. W., D. A. Andrews, and C. Y. Manuel-Faler. 1983. Application of island biogeographic theory to streams: macroinvertebrate recolonization of the Teton River, Idaho, p. 279–297. *In* J. R. Barnes and G. W. Minshall [ed.] Stream ecology: application and testing of general ecological theory. Plenum, New York, NY.

Minshall, G. W., and J. N. Minshall. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain stream. Hydrobiologia 55: 231–249.

Minshall, G. W., and R. C. Petersen. 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. Arch. Hydrobiol. 104: 49–76.

Morin, A. 1987. Unsuitability of introduced tiles for sampling black fly larvae. Freshwater Biol. 17: 143–150.

Narf, R. P. 1985. Aquatic insect colonization and substrate changes in a relocated stream segment. Great Lakes Entomol. 18: 83–92.

Ogilvie, G. 1988. The effects of periphyton manipulations on the microdistribution of grazing macroinvertebrates. Verh. Int. Ver. Limnol. 23: 1101–1106.

Osborne, L. L. 1983. Colonization and recovery of lotic epilithic communities: a metabolic approach. Hydrobiologia 99: 29–36.

Otto, C., and P. Sjöström. 1985. Behavior of drifting insect larvae. Hydrobiologia 131: 77–86.

Parker, M. S. 1989. Effect of substrate composition on detritus accumulation and macroinvertebrate distribution in a southern Nevada desert stream. Southwest. Nat. 34: 181–187.

Peckarsky, B. L. 1980. Influence of detritus upon colonization of stream invertebrates. Can. J. Fish. Aquat. Sci. 37: 957–963.

1985. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? Can. J. Zool. 63: 1519–1530.

1986. Colonization of natural substrates by stream benthos. Can. J. Fish. Aquat. Sci. 43: 700–709.

Peckarsky, B. L., and S. I. Dodson. 1980. Do stonefly predators influence benthic distributions in streams? Ecology 61: 1275–1282.

Pianka, E. R. 1970. On *r*- and *k*-selection. Am. Nat. 104: 592–597.

Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environ. Manage. 14: 629–645.

Pontasch, K. W., and M. A. Brusven. 1987. Periphyton response to a gasoline spill in Wolf Lodge Creek, Idaho. Can. J. Fish. Aquat. Sci. 44: 1669–1673.

1988. Macroinvertebrate response to a gasoline spill in Wolf Lodge Creek, Idaho, USA. Arch. Hydrobiol. 113: 41–60.

Poole, W. C., and K. W. Stewart. 1976. The vertical distribution of macrobenthos within the substratum of the Brazos River, Texas. Hydrobiologia 50: 151–160.

Rabeni, C. F., and G. W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. Oikos 29: 33–43.

Reice, S. R. 1984. The impact of disturbance frequency on the structure of a lotic riffle community. Verh. Int. Ver. Limnol. 22: 1906–1910.

1985. Experimental disturbance and the maintenance of species diversity in a stream community. Oecologia 67: 90–97.

Resh, V. H. 1982. Age structure alteration in a caddisfly population after habitat loss and recovery. Oikos 38: 280–284.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. Wissmar. 1988. The role of disturbance in stream ecology. J. N. Am. Benthol. Soc. 7: 433–455.

Richards, C., and G. W. Minshall. 1988. The influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream. J. N. Am. Benthol. Soc. 7: 77–86.

Robinson, C. T., and G. W. Minshall. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. J. N. Am. Benthol. Soc. 5: 237–248.

Rosenberg, D. M., and V. H. Resh. 1982. The use of artificial substrates in the study of freshwater benthic macroinvertebrates, p. 175–235. *In* J. Cairns [ed.] Artificial substrates. Ann Arbor Science Publishers, Ann Arbor, MI.

Rounick, J. S., and M. J. Winterbourn. 1983. The formation, structure and utilization of stone surface organic layers in two New Zealand streams. Freshwater Biol. 13: 57–72.

Sagar, P. M. 1983. Invertebrate recolonization of previously dry channels in the Rakaia River. N.Z. J. Mar. Freshwater Res. 17: 377–386.

1986. The effects of floods on the invertebrate fauna of a large, unstable braided river. N.Z. J. Mar. Freshwater Res. 20: 37–46.

Scrimgeour, G. J., R. J. Davidson, and J. M. Davidson. 1988. Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. N.Z. J. Mar. Freshwater Res. 22: 337–344.

Scrimgeour, G. J., and M. J. Winterbourn. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand River. Hydrobiologia 171: 33–44.

Shaw, D. W., and G. W. Minshall. 1980. Colonization of an introduced substrate by stream macroinvertebrates. Oikos 34: 259–271.

Sheldon, A. L. 1984. Colonization dynamics of aquatic insects. p. 401–429. *In* V. H. Resh and D. M. Rosenberg [ed.] The ecology of aquatic insects. Praeger Publishers New York, NY.

Siegfried, C. A., and A. W. Knight. 1977. The effects of washout in a Sierra foothill stream. Am. Midl. Nat. 98: 200–207.

Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. Annu. Rev. Ecol. Syst. 5: 161–182.

Söderström, O. 1987. Upstream movements of invertebrates in running waters — a review. Arch. Hydrobiol. 111: 197–208.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. 15: 353–392.

Stites, D. L., and A. C. Benke. 1989. Rapid growth rates of chironomids in three habitats of a subtropical blackwater river and their implications for *P–B* ratios. Limnol. Oceanogr. 34: 1278–1289.

Strong, D. R., D. Simberloff, L. G. Abele, and A. B. Thistle [ed.] 1984. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, NJ. 613 p.

Towns, D. R. 1981. Life histories of benthic invertebrates in a Kauri forest stream in northern New Zealand. Aust. J. Mar. Freshwater Res. 32: 191–211.

Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. J. N. Am. Benthol. Soc. 8: 36–50.

Townsend, C. R., and A. G. Hildrew. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. J. Anim. Ecol. 45: 759–772.

Ulfstrand, S., L. M. Nilsson, and A. Stergar. 1974. Composition and diversity of benthic species collectives colonizing implanted substrates in a South Swedish stream. Entomol. Scand. 5: 115–122.

Wallace, J. B. 1990. Recovery of lotic macroinvertebrate communities from disturbance. Environ. Manage. 15: 605–620.

Wallace, J. B., D. S. Vogel, and T. F. Cuffney. 1986. Recovery of a headwater stream from an insecticide-induced community disturbance. J. N. Am. Benthol. Soc. 5: 115–126.

Waters, T. F. 1964. Recolonization of denuded stream bottom areas by drift. Trans. Am. Fish. Soc. 93: 311–315.

1972. The drift of stream insects. Annu. Rev. Entomol. 17: 253.

Wiens, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes, p. 439–457. *In* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle [ed.] Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, NJ.

Wiley, M. J., and S. L. Kohler. 1981. An assessment of biological interactions in an epilithic stream community using time-lapse cinematography. Hydrobiologia 78: 183–188.

Williams, D. D. 1977. Movements of benthos during the recolonization of temporary streams. Oikos 29: 306–312.

1980. Temporal patterns in recolonization of stream benthos. Arch. Hydrobiol. 90: 56–74.

Williams, D. D., and H. B. N. Hynes. 1976. The recolonization mechanisms of stream benthos. Oikos 27: 265–272.

Williams, D. D., and J. H. Mundie. 1978. Substrate size selection by stream invertebrates and the influence of sand. Limnol. Oceanogr. 23: 1030–1033.

Winterbourn, M. J. 1978. The macroinvertebrate fauna of a New Zealand forest stream. N.Z. J. Zool. 5: 157–169.

Winterbourn, M. J., B. Cowie, and J. S. Rounick. 1984. Food resources and ingestion patterns of insects along a West Coast, South Island, river system. N.Z. J. Mar. Freshwater Res. 18: 43–51.

Winterbourn, M. J., A. G. Hildrew, and A. Box. 1985. Structure and grazing of stone surface organic layers in some acid streams of southern England. Freshwater Biol. 15: 363–374.

Winterbourn, M. J., J. S. Rounick, and B. Cowie. 1981. Are New Zealand stream ecosystems really different? N.Z. J. Mar. Freshwater Res. 15: 321–328.

Wise, D. H., and M. C. Molles. 1979. Colonization of artificial substrates by stream insects: influence of substrate size and diversity. Hydrobiologia 65: 69–74.

ANNOUNCEMENTS/AVIS

The Ecological Effects Branch, Office of Pesticide Programs (OPP), Environmental Protection Agency (EPA), currently collects fish and wildlife incident data related to pesticide use. We are interested in all information related to incident kills in North America associated with the use of pesticides. Please report these incidents to Daniel Rider or Candace Brassard, Ecological Effects Branch, OPP, EPA, 401 M St. SW, H5707-C, Washington, DC 20460, USA, or call (703) 305-5314/305-5392; FAX (703) 305-6309.

La *Ecological Effects Branch* de l'*Office of Pesticide Programs* de l'*Environmental Protection Agency* (EPA) procède actuellement à la collecte de données sur des incidents relatifs aux effets de pesticides sur le poisson et la faune. Nous sommes intéressés à obtenir tout renseignement ayant trait à des hécatombes liées à l'utilisation de pesticides. Veuillez communiquer vos renseignements à ce sujet à Daniel Rider ou Candace Brassard par courrier adressé à la *Ecological Effects Branch*, OPP, EPA, 401 M St. SW, H5707-C, Washington, DC 20460, USA, ou par téléphone (703) 305-5314/305-5392; télécopieur : (703) 305-6309.

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 49, No. 3, March 1992 Volume 49, n° 3, mars 1992

Schnute, J. T. Statistical analysis of embedded replicates in mark–recovery experiments 432–442

Staurnes, M., T. Sigholt, G. Lysfjord, and O. A. Gulseth. Difference in the seawater tolerance of anadromous and landlocked populations of Arctic char (*Salvelinus alpinus*) 443–447

Schmitz, M. Annual variations in rheotactic behaviour and seawater adaptability in landlocked Arctic char (*Salvelinus alpinus*) 448–452

Ogura, M., and Y. Ishida. Swimming behavior of coho salmon, *Oncorhynchus kisutch*, in the open sea as determined by ultrasonic telemetry 453–457

Varnavsky, V. S., T. Sakamoto, and T. Hirano. Stunting of wild coho salmon (*Oncorhynchus kisutch*) in seawater: patterns of plasma thyroid hormones, cortisol, and growth hormone 458–461

Martin, A. R., and T. G. Smith. Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas* 462–466

Frank, K. T., J. W. Loder, J. E. Carscadden, W. C. Leggett, and C. T. Taggart. Larval flatfish distributions and drift on the southern Grand Bank 467–483

Polacheck, T., D. Mountain, D. McMillan, W. Smith, and P. Berrien. Recruitment of the 1987 year class of Georges Bank haddock (*Melanogrammus aeglefinus*): the influence of unusual larval transport 484–496

Grafton, R. Q. Rent capture in an individual transferable quota fishery 497–503

Hill, W. R., H. L. Boston, and A. D. Steinman. Grazers and nutrients simultaneously limit lotic primary productivity 504–512

Marcogliese, D. J. *Neomysis americana* (Crustacea: Mysidacea) as an intermediate host for sealworm, *Pseudoterranova decipiens* (Nematoda: Ascaridoidea), and spirurid nematodes (Acuarioidea) 513–515

Goddard, S. V., M. H. Kao, and G. L. Fletcher. Antifreeze production, freeze resistance, and overwintering of juvenile northern Atlantic cod (*Gadus morhua*) 516–522

Boisclair, D. An evaluation of the stereocinematographic method to estimate fish swimming speed 523–531

Morin, A. et N. Bourassa. Modèles empiriques de la production annuelle et du rapport *P/B* d'invertébrés benthiques d'eau courante 532–539

Bilby, R. E., and P. A. Bisson. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams 540–551

Bozek, M. A., and F. J. Rahel. Generality of microhabitat suitability models for young Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) across sites and among years in Wyoming streams 552–564

Hudon, C., D. G. Parsons, and R. Crawford. Diel pelagic foraging by a pandalid shrimp (*Pandalus montagui*) off Resolution Island (eastern Hudson Strait) 565–576

Jones, R. D., and J. A. Amador. Removal of total phosphorus and phosphate by peat soils of the Florida Everglades 577–583

Bayley, S. E., D. W. Schindler, K. G. Beaty, B. R. Parker, and M. P. Stainton. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus 584–596

Beauchamp, J. J., S. W. Christensen, and E. P. Smith. Selection of factors affecting the presence of brook trout (*Salvelinus fontinalis*) in Adirondack lakes: a case study 597–608

Morris, J. T., and B. C. Coull. Population dynamics, numerical production, and potential predation impact on a meiobenthic copepod 609–616

Reviews/Synthèses

Mackay, R. J. Colonization by lotic macroinvertebrates: a review of processes and patterns 617–628

Announcements/Avis 629

© Minister of Supply and Services Canada 1992
Ministre des Approvisionnements et Services Canada 1992

CJFSDX49(3)431–629 (1992)
ISSN 0706-652X

Subscription rates/Abonnements

Canada: Institutional/Collectif $275; Personal/Personnel $95
Other countries/Autres pays : Institutional/Collectif $330(U.S.); Personal/Personnel $114(U.S.)
Single issue/Par numéro : $16.95 (Canada); $20.35(U.S.) (Other countries/Autres pays)